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Old-growth forests are structurally complex in both vertical and horizontal dimensions. This complexity arises from biological characteristics, typically branch and leaf structure, but also includes epiphytes with varying form and function. I characterized the biomass and species composition of epiphytes along the vertical axis of an old-growth Douglas-fir (*Pseudotsuga menziesii*) tree called the Discovery Tree (~60 m tall, estimated age 300 years). Epiphyte biomass was estimated approximately every 10m on both the trunk and the branches attached in a given zone, using calibrated visual estimates. The highest total epiphyte biomass and species richness was found at 30 m; the upper canopy had reduced bryophyte biomass, but an increased presence of lichens dominated, while the lower canopy had much less epiphytic biomass. The common genera (*Dicranum, Neckera, Porella*, and *Isothecium*) were used in a greenhouse watering and drying experiment to assess water retention of each species. Taxa that tend to be associated with old-growth forests (*Dicranum* and *Neckera*) had greater water absorption and longer durations of water retention by up to 2 days in a simulated 60 mm rain event. By retaining and storing more water in the canopy, these bryophytes may alter rates of evaporation, heating, and cooling, potentially buffering microclimates from extremes. The bryophyte drying experiment suggests that bryophyte species will affect its role in canopy water retention and evaporation.

To characterize microclimate gradients associated with these epiphytes, I installed microclimate sensors along the vertical axis of the same Douglas-fir tree at six microclimate stations, located 1.5, 10, 20, 30, 40 and 56 m above ground. These sensors measured air temperature, relative humidity, wind speed and direction, and leaf surface wetness from (August 2, 2016 – July 31, 2017), and I analyzed the data at the daily and quarter-monthly time scales. Using leaf wetness and temperature data, I used times-series cluster analysis and generalized additive models to assess how the microclimate stations differed and to establish zones within the canopy that had relatively consistent values among the microclimate stations. I classified canopy zones (low, middle and upper canopy) for four representative months (August, November, February and May). Canopy zones changed in size and relative values across seasons. The upper canopy experienced a greater range of microclimate variability than the lower canopy. In each of the four months, 56 m was identified as the only microclimate station in the upper canopy, while the middle and lower canopy zones expanded and contracted depending on the time of year. Relative humidity variation was greater at the top of the canopy than the lower canopy. Wind speed was much greater and consistently from the east at the top of the canopy, while the lower canopy has much lower wind speeds which came at different directions.

Monitoring microclimates in conjunction with the bryophyte assessment allows for conjecture on feedbacks between the microclimate and vegetation. Because bryophytes that tend to be associated with old-growth forests held water longer, we can speculate that this increased water retention feeds back into the microclimate by buffering temperatures. This study also shows that the seasonality of microclimate partitioning may be an important factor in understanding vertical bryophyte distribution and potential climate feedbacks.

Canopy microclimates and epiphytes: Examining dynamic patterns and influences

by
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INTRODUCTION

Old-growth forests have a suite of characteristics that make them structurally complex systems, both vertically and horizontally (Franklin and Van Pelt 2004). Vertically the forest has a continuous or multi-layered canopy with a dense understory; horizontally, gap dynamics, canopy openings and dense regrowth are the main driver of heterogeneity (Franklin and Van Pelt 2004). Forest structural complexity increases with age, not only because the accumulation of branches and multi-aged tree boles leads to greater complexity, but also because older forests are able to reach heights unattained by younger forests (Franklin et al. 2002, Boyden et al 2005, Halpern and Lutz 2013). The structural complexity typical of old-growth trees creates microclimates with unique temperature and moisture regimes (Baker et al. 2014).

Many regions of the globe are rapidly warming, and the Pacific Northwest (PNW) is predicted to have a 2°C average temperature increase by 2100 (US Fish and Wildlife 2011). However, old-growth forests are protected in the PNW (Davis et al 2015), and maintain a diversity of microclimates within these complex forests, which may be an important feature of the region's resilience (Frey et al 2016). Microclimates in the upper canopy are often decoupled from the understory (Szarzynski and Anhuf 2001, Pypker et al. 2007a), meaning that the upper canopy experiences microclimate conditions distinct from the middle or lower canopy, for example it can be hot and dry in the upper canopy but cool and wet in the lower canopy. Because global temperature averages are taken using satellite data and open-field weather station data, temperature regimes within the understories of old-growth forest are not tracking with global averages (Storlie et al 2014, Frey et al 2016). For example, at the HJ Andrews Experimental

Forest (HJA) in Oregon, sub-canopy climate measurements within old growth Douglas-fir forests have not followed the same pervasive temperature increase that has been recorded regionally (Frey et al 2016). With increasing temperatures, the 2.5°C cooler temperatures in the understory of an old-growth forests could be critical to survival of many species (Frey et al. 2016). The species that live above 1.5 m will also rely on microclimates to ease their adaptation to climate change, but the amount of protection, or the degree of decoupling of the canopy, afforded by microclimates to these species is unknown. It is hard to characterized the vertical profiles of canopy microclimates because vertical transects of forest canopy microclimate data are rare. This information gap is due to the logistical challenges of collecting detailed microclimate measurements throughout the canopy and is further complicated by the fact that microclimate trends and variations may differ among the canopies of different forest types.

In this study, we evaluated two related phenomena. The first phenomenon is the microclimate pattern along the vertical axis of a Douglas-fir tree within an old-growth Douglas-fir and western hemlock forest at the HJ Andrews, and the tendency for the upper canopy to have higher microclimate variability than the lower canopy. The second phenomenon is the influence of epiphytes on microclimate. By first looking at the characterization of the microclimate profile, we sought to characterize how the microclimate varies along a vertical transect. We then evaluated the ability of epiphytic species to retain water and alter their environment, making it possible to examine the existence of a feedback between bryophytes and microclimate gradients. Microclimates have been used as predictor variables of ecological phenomena, but they are also themselves the result of ecological phenomena: the complex interactions of stand age, structure and vegetation. By looking at how structure and vegetation influence the microclimate and species community development, links between community and microclimate can be made in both directions.

MICROCLIMATE

In this study, a microclimate is defined as the localized meteorological measurements (including air temperature, relative humidity, leaf wetness, wind speed and direction) that may or may not differ from the ambient conditions. Forest microclimate is generally decoupled from the larger-scale climate typically measured at weather stations (Hayden 1998). Radiation, evaporative cooling, canopy cover and boundary layer effects interact to alter the conditions occurring at small scales (Jones 1992, Hayden 1998).

Climate data from weather stations are frequently used to inform ecological studies; however, the resolution of climate variables measured at these stations is not intended to detect differentiation of small-scale processes across a landscape (Hayden 1998). Like climate measurements, microclimates determine processes and ecosystem functions, but at a very local scale, and can drive niche partitioning within a system (Ma et al 2010, Frego 2007). Additionally, microclimates have been shown to serve as refugia for species, particularly during the hottest part of the day (Scheffers et al. 2014).

While the scale of microclimates is variable, the majority of small organism experience these microclimates rather than the macroclimate that larger organisms experience (Lindo and Winchester 2013). In one example of insect interactions with microclimate; Dial et al. (2006) found a correlation between humidity and arthropod abundance. For species that are easily desiccated, moist microclimates are critical to survival, limiting their dispersal to the sunnier, hotter, dryer upper canopy (Dial et al. 2006). A similar pattern of increased insect herbivory occurred in the cooler lower canopy (Shaw et al.1006). Additionally, epiphytic lichens and bryophytes are used as indicators of different microclimatic regimes in the canopy (McCune 1993, Rambo and Muir 1998, Frego 2007, Batke et al. 2015). The relationships among insects, epiphytes, pathogens, and microclimates are even utilized in agriculture to reduce the need for pesticides by manipulating plant structures to encourage air flow (Tivoli et al. 2013). The influence of plant structure on microclimate is strong enough that weather station data does not necessarily represent what organisms experience. With pending temperature increases, microclimates could experience more extreme variation in temperature under some conditions while acting as buffers under other conditions.

ABIOTIC INFLUENCES ON MICROCLIMATE

Traditionally, temperature, relative humidity and/or light intensity are used to measure microclimates as they are the key drivers of most processes (Ma et al. 2010, Szarzynksi and Anuf 2001).

Air temperature, surface thermal temperature (Kim et al. 2016) and the relationship between the two are important considerations for microclimate studies. Air temperature influences evaporation and transpiration rates, as it is the measure of heat energy present in a system (Jones 1992). Surface temperature reflects more closely what organisms are experiencing and thus they are required to respond, such as changes in transpiration rates in leaves or activity levels by insects in response to temperature changes (Schmitz 1996). Air and surface temperatures are correlated, but have variable lags in time between them depending upon irradiance, capacitance and albedo. Taken together, the air temperature (sensible heat) and leaf temperature (radiant heat) can compute canopy thermal conductance and relate how oxygen, carbon dioxide, and water vapor move throughout a canopy (Jones 1992). A relevant example is dewfall in the canopy. At night, when the surface temperature of a leaf decreases due to the lack of incoming radiation, net radiation from the leaf becomes negative, and it begins to lose heat. As the leaf cools to below air temperature, condensation occurs on the leaf and a dewfall event occurs (Jones 1992). Condensation reactions could have large effects on the canopy water budget, if they absorb and retain the condensation (Pypker et al. 2016) that is incited by the air and surface temperature differentials.

Dewfall is related to relative humidity, which is the percent moisture content of the air compared to its saturation level at that temperature. As temperature decreases, the amount of water that can be stored in an air mass decreases. Condensation occurs when the temperature reaches a point at which the vapor pressure is equal to the saturation vapor pressure (Jones 1992).

Relative humidity is important to the water budget for both epiphytes and terrestrial plants. Water stress is often lower when relative humidity is high because transpirations rates decrease. Some species of lichen are even able to absorb enough water vapor to photosynthesize when relative humidity is high enough (Campbell and Coxson 2001, Pypker et al 2016). Dewfall may be required for bryophytes for photosynthesis to begin in the summer (Chapter 2). Because bryophytes and lichens are poikilohydric and can oscillate between desiccated and hydrated states, a condensation event can provide water to reactivate photosynthesis for these organisms (Lakatos 2011).

Because dewfall is difficult to measure, it is challenging to assess the frequency and magnitude of such events using only air temperature and relative humidity measurements (Jones 1992). By contrast, leaf wetness sensors use the dielectric method to determine when water is sitting on the leaf surface. The leaf wetness sensors can also diagnose the quantity of water deposited in the canopy and how long it remains (Klemm et al. 2002). Canopy water storage capacity is an important feature of old-growth forests and is greatly enhanced by the presence of epiphytes, which have both internal and external water storage (Pypker et al. 2006). The leaf wetness measurement is not a perfect proxy for canopy water storage in old-growth Douglas-fir forests, as a) it does not estimate internal water, and b) the sensor doesn't have an identical boundary layer, or profile of absorption or radiation of energy, to a leaf or other structure of interest, in this case, bryophytes, which themselves vary in physical characteristics. However, it is able to provide data on precipitation and condensation events, such as rain and dewfall, respectively (Klemm et al. 2002). However, it is difficult to distinguish condensation events from precipitation events, and leaf wetness data is complemented by rain gauge data. While the leaf wetness sensor might not be the most accurate measurement to estimate canopy storage, it can be used to estimate how long a rain or condensation event affects the canopy, especially when sensors are stratified throughout the canopy (Klemm et al. 2002, Calder 2001). Rain gauges are able to report on the total amount precipitated; however, through-fall can alter these determinations and raindrop size can affect the retention and interception of water in the canopy Calder (2001). Leaf wetness is correlated with relative humidity and precipitation; however, it provides additional information (timing and relative magnitude of surface wetting), for understanding the hydrologic cycle of the canopy that would be otherwise overlooked.

Wind speed and direction influence evaporation rates, air and surface temperature, and canopy conductance. Increased wind speeds can increase the rate of evaporation; however, wind can have an alternative effect if temperatures are high. Wind could increase convective cooling of surfaces, lowering their temperatures, which could in turn reduce evapotranspiration rates

(Jones 1992). Additionally, increasing wind speed can reduce the resistance of the boundary layer, leading to less stable environments below (Jones 1992). Jones (1992) noted that gusts of wind can form eddies that span from above the canopy to the forest floor. Wind gusts are responsible for 50% of energy transfer, while only accounting for 5% of the events detected by upper canopy and lower canopy paired sensors. When pairs of anemometers are taken together; for example, when wind at the top of the canopy is moving in a different way than wind at the forest floor, topography, vegetation structure and other features of the landscape are likely influencing the flow of air through the forest. The same can be said for wind speed, which will be higher above the canopy than below; certain features of the landscape are buffeting the air mass and slowing it down as it moves throughout the forest beneath the canopy (Jones 1992). In this study, the boundary layer wind speeds could not be measured due to logistical constraints; however, the upper anemometer is able to track the forces of wind hitting a tall canopy tree.

Finally, soil temperature and moisture are measured at the site, but are less of a concern for the suite of parameters important for canopy water storage. However, there has been extensive research into the microclimates of soils to enhance knowledge of site productivity and biogeochemical cycles (Xu et al 2004, Ma et al 2010). Soils are also important factors in the energy balance of the forest, storing and releasing water that is incorporated into the canopy hydrology (Pypker et al. 2106). The old growth forests at the HJ Andrews are characterized by deep soil horizons (Sun et al 2004), and soil temperature can inform how decomposition rates change as you move through the organic and mineral layers (Christenson et al. 2010). Soil moisture is important to understand water stress of plants; however, this aspect of the microclimate was not addressed in this study.

When taken in concert, the suite of measurements can help to elucidate the processes occurring in the canopy that are difficult to measure from the ground or from above. In contrast to the relatively large number of studies that characterize understory microclimates of old-growth forests (Richardson et al. 2004, Heithecker and Halpern 2007, Ma et al. 2010 Frey et al. 2016), this study is one of very few to investigated microclimate in Pacific Northwest old-growth forest at multiple heights. Microclimates are critical to ecosystem function because they provide refuge while species adapt to climate change (Potter et al 2013). Having a baseline understanding of microclimate patterns throughout the canopy is critical to future management. While it is impossible to control many of the abiotic factors that are influencing climate change, the structure of the forest may be one way in which managers can take an active approach to microclimate conservation and even cultivation.

INFLUENCE OF FOREST STRUCTURE ON MICROCLIMATE

The structure of the forest is the aboveground skeleton on which ecosystems are built. The architecture of the trees and the orientation of their branches, trunks, leaves, deadwood and roots influence microclimate (Saudreau et al. 2013). Topography also has a strong effect on microclimate (Xu et al. 2004, Daly et al 2009, Frey et al 2016), but for the purpose of this study, vertical change will be concerned with tree height effects.

The general relationship between time since disturbance and typical structure of forests has been well established: forest structure becomes more complex as the forest ages (Franklin et al. 2002, Boyden et al 2005, Halpern and Lutz 2013). As forests age, their net primary productivity (NPP) follows a roughly logistic curve (Larson et al. 2008, McKinley et al. 2011). With increasing productivity, trees create more biomass, and gap formation disrupts complete canopy closure allowing the understory to develop. Over time, the accumulation of NPP products, i.e., branches and tree boles, leads to older forests having a greater structural complexity and density (defined as the amount of biomass in a volume of space) in their lower canopies, while younger forests have a higher canopy density in their upper canopy zone. Evidence from LiDAR (Light Detection and Ranging) data show this shift in complexity as a forest ages (Lefsky 2002). This change in canopy level density is a direct function of age; as the older branches die off and fall to the ground, the decomposing wood and increased light foster a rich understory, increasing the structural density (Reilly and Spies 2015).

The upper canopy of a forest consists of a markedly different ecosystem than what exists below (Magrach and Santamaría 2013, Didham and Ewers 2014). In general, the upper canopy is brighter, hotter, drier and windier than the below-canopy measurements. Specific patterns within forests vary depending upon factors such as species composition, topography and climatic regime (Hayden 1998). The upper canopy receives direct solar radiation, which is filtered through leaves, branches, and epiphytes to reach the lower canopy. Depending upon the height of the canopy and the degree of layering within, the diffusion of light will vary at the forest floor (Badano et al. 2015). The direct radiation of the upper canopy leads to increased temperature both in the air and on the vegetation surface. During the day, air temperature is increased due to radiant heat loss held within the boundary layer above the vegetation (Jones 1992) The surface temperature can be much hotter than the air temperature (Saudreau et al. 2013), leading to a higher vapor pressure deficit and a more desiccated environment (Szarynski and Anhuf 2001). Evaporation and transpiration tend to be higher at the top of the canopy as a result of the increased temperature and vapor pressure deficit (Szarynski and Anhuf 2001, Magrach and Santamaría 2013). The increased water in the canopy usually does not increase relative humidity dramatically in the daytime, but continued evaporation throughout the night can increase humidity and decrease temperature (Pypker et al 2016). Epiphytes on trees serve as an indicator of the upper canopy's distinct microclimate; lichens tend to be located at the top of the tree, being able to withstand the hotter, dryer conditions, and bryophytes tend to be located in the more sheltered, moister, cooler parts of the canopy (McCune 1993).

Wind can complicate these general patterns. In an even canopy forest, the boundary layer above will be well established and mixing throughout the canopy will be minimal (Jones 1992). In a complex canopy, airflows become more turbulent and mixing throughout the canopy is more likely to occur (Jones 1992). Additionally, forests with dense canopies have much more stable airflows relative to open canopies or forests with a dense upper canopy but open understory (van Gorsel et al. 2011). The same is true within complex canopies, in which airflow and turbulence differ as a function of canopy height. Old-growth forests have moderated airflows in their lower canopy, making the effect of above canopy air movements less dramatic; the highest frequency airwaves are rapidly filtered, leaving only slower air waves to enter the system. Notably, each type of canopy has a different effect on airflow and wave radiation (Rambo and North 2008), and so there is considerable uncertainty in extrapolation from a study in one forest to another.

Microclimates are difficult to predict accurately because they have a great deal of heterogeneity across gradients (Xu et al 2004). Parameters can vary at different scales, such as wind at the kilometer scale or soil moisture at the meter scale (Anderson et al 2007). Additionally, microclimate data are traditionally the result of spatial and temporal autocorrelation (Xu et al 2004). These two metrics of data structure are inherent to microclimates themselves. The variation is due to the heterogeneity of the landscape, species living on the landscape (influencing evapotranspiration rates, for example), and larger topographic features

(Xu et al. 2004, Hayden 1998). The autocorrelation of microclimate is again dependent on the scale at which each is being analyzed, but temporally some variables have greater memory than others, meaning the conditions of the past are likely to influence the current state. High amounts of water in the system could increase the memory of many variables, such as leaf wetness, relative humidity and temperature, due to a decreased evaporation rate (Hayden 1998). The degree of spatial autocorrelation among variables along the vertical gradient is likely reduced compared to a horizontal transect due to the dramatic difference in water availability between the upper and lower canopy (Szarzynski and Anuf 2001).

However, many studies have examined the edge effects of forests on microclimates, and the increased heterogeneity edges bring into a system's microclimate. Edges, much like canopies, are the first buffer zone of forest. While the canopy of an old-growth forest is structurally complex, the openness of the upper canopy to light is analogous to that of an edge. Both boundaries let light in further than an even-aged stand or a closed forest (Magrach et al 2013, Baker et al 2014, Didham and Ewer 2014).

Using edges as a well-studied analogous structure to canopies provides a baseline to compare the scale of variable correlation and the intensity of the gradient caused by each structure. For example, Baker et al (2014) found that the magnitude of influence a forest edge has on microclimate was seasonally dependent, and that microclimates should be assessed seasonally to track shifts. However, edges are necessarily limited in their ability to address microclimate gradients at the forest core, and therefore canopies must be considered. Magrach and Santamaría (2013) investigated the relationship between forest edge and canopy with regard to epiphyte distribution and success, finding that gradients going horizontally into the forest towards a core are similar to those going vertically from the canopy. The driving importance of light and humidity on microclimate meant that the core forest canopy was more favorable than an edge for their target species, needing both high light and humidity (Magrach and Santamaría 2013). The effect of edge has been reported to be up to one tree height in length to the forest (Baker et al. 2014), meaning that from the core of a forest, the gradient from the top of the canopy to the forest floor is steeper than that from an edge. Therefore, the canopy gradient must occur in less than the 40-60 meters that a lateral edge influences microclimate (Laurance et al 2002 as cited by Magrach et al 2013).

The underlying structure of a forest is integral to the microclimates that can exist. Old-growth forests have been found to maintain these microclimates better than second growth-forests (Frey et al. 2016), adding to the myriad of ecosystem services old-growth forests provide. For example, an old-growth Douglas-fir tree provides habitat all along its trunk, spanning upwards of 50 meters. The species that live in those habitats are subjected to a range of climates from the upper canopy to the forest floor, with variation due to factors such as cardinal direction, branch presence, and neighboring tree shading (Einzmenn et al 2014, Taylor and Burns 2016). Understanding how the structure of a forest influences its microclimate distribution is critical with a changing climate. The macroclimate influences can be buffered and buffeted by the forest to create pockets of refugia and potentially ease the climate transition. These microclimate refuges will be of paramount importance to the epiphytes.

EPIPHYTE FEEDBACKS ON MICROCLIMATE

Microclimates are closely tied to epiphyte species composition. The relationship between height and species composition is well established (McCune 1993), but an interactive relationship between epiphytes and their microclimates is still being explored (Stuntz et al 2002, Stanton et al 2014). Epiphytes have the capacity to greatly increase canopy water storage with mosses storing up to 10-15 times their dry weight and lichens storing up to 2-3 times (Pypker et al 2006). In the PNW, most epiphytic bryophytes store their water externally, meaning they are able to large amounts of water on their surface. Old-growth forests are able to store more water in their canopies than second growth forests, which do not have as complex epiphyte communities. Old-growth forests take much longer to dry than younger forests (Rambo and North 2008); the extra water held in the canopy by epiphytes may be contributing to this pattern.

Not only do epiphytes increase the amount of water stored in the canopy (Pypker et al. 2016), but they might actually increase water retention in storm events as well (Pypker et al 2006). Leaf wetness is inversely related to the size of a raindrop, where heavier raindrops decrease leaf wetness and lighter raindrops increase water retention on leaves (Calder 2001). However, the architecture of moss may minimize the effect of drop size because the water drop is slowed by the outer leaves of the bryophyte and then absorbed by the mat itself (Glime 2013a). Increasing total water storage has undoubted effects on microclimate and a positive-feedback loop between the epiphytes and microclimate has been proposed but as of yet unquantified (McCune 1993). It is likely that type of relationship, passive or interactive, between microclimates and epiphytes is dynamic throughout the canopy due to species distributions of lichens and bryophytes (McCune 1993). Lichens typically colonize harsher environments in the upper canopy (McCune 1993, Gauslaa 2014), and while lichen water storage is sufficient to allow them to grow in harsh environments, it would not be enough to influence its microclimate. Bryophytes can store much more water (Pypker 2006) and in the PNW are sheltered from the harsh conditions experienced in the upper canopy, potentially enabling an interactive relationship with the local microclimate.

An interactive relationship between bryophytes and microclimates is grounded in their water storage capacity; however, bryophytes effect temperature as well as relative humidity. Thermal images at our HJ Andrews study site suggest that the old-growth forest canopy remains cooler than the adjacent secondary growth forest (Kim et al. 2015). Epiphytes have also been found to keep branches cooler during the daytime (Freiberg 2001). These two thermal patterns suggest that epiphytes contribute to the moderation of tree temperatures in old growth forests (Stuntz et al. 2002). Other strong contributors to temperature moderation in old-growth forests are evaporation rates and leaf area index (Muñoz-Villers et al. 2012, von Arx et al. 2013).

The sensitivity of epiphytes to microclimates supports the idea that not only are epiphytes having an effect on their own habitat, but that abiotic conditions must be present to facilate epiphyte establishment before epiphytes can begin to feed back into the ecosystem. Epiphytes colonize from the ground up (McCune et al. 2000). Epiphytes access the canopy by having their populations expand upward and outward (on branches) as the tree grows, so that lichens, in particular, are continually colonizing new habitats (Johansson 2008). Once a suitable habitat is found, then the feedback into the microclimate begins and species interactions diversify the population, such as birds bringing in propagules of different epiphyte species (McCune et al 2000). This protracted successional process is due to the epiphyte mats growing extremely slowly and having a high sensitivity to change (Frego 2007).

The reproductive strategy and life history of epiphytic mosses is important to consider when assessing their ability to contribute to microclimate stability (Glime 2013). Bryophytes, typically classified as a homogenous group in epiphyte studies, can be classified by their structural aspects and life-history strategies. Epiphytic bryophyte diversity in the PNW is limited to a few species, and this study focuses on four common species: *Dicranum fuscenscens,* *Isothecium stoloniferum, Neckera douglasii* and *Porella navicularis*. The ability to store water is closely tied to life history and growth structure. Two of the species, *Isothecium* and *Porella*, are early colonizers of forests (Muir et al 2006, Jonsson 1996). These two species are quick to cover trunks and branches, but in older forests are frequently found below mats, either along the edge or as dead biomass below the mat of more competitive moss species.

While the early colonizing genera *Isothecium and Porella* proceed upwards until the conditons becomes too hot and dry, the slower colonizing species begin to establish themselves. *Neckera* and *Dicranum* have more complexity to their structures than *Isothecium* and *Porella. Neckera* looks superficially similar to *Porella*, but has a higher degree of branching and leaves (Jonsson 1996). The mats of *Neckera* have smaller air pockets than those of *Porella,* which likely results in reducing airflow within the mat and conserving water. (Glime 2013a) *Dicranum* is even denser but has a tuft/pin-cushion structure (Glime 2013a). New growth develops out of continuingly elongating shoots that are short and dense. *Dicranum* grows directly on the bark, adhering extremely closely, so that it accesses water that runs down the trunk, as well as the water that it collects on its leaves. It is also able to capitalize on the vertical trunk space, which is unavailable to other species because they get too large to stay adhered; large mats of *Neckera* and *Porella* generally are found on branches or sloping trunks (Glime 2013a). *Isothecium* has a flagelliform life form and is able to adhere on the vertical trunk and hang in wisps below branches (Glime 2013a),.

Many of the features that make *Porella* and *Isothecium* strategic colonizers make them easy to outcompete. While their energy is put into reproduction and fast growth, *Neckera* and *Dicranum* slowly advance (Kimmerer 2003). The density of a moss is positively related to its long-term success (Glime 2013b). *Neckera* and *Dicranum* are both considered K-strategists, doing best in stable environments with low stress, while *Porella* and *Isothecium* are considered "bet-hedgers" competing best when environmental conditions are more variable. (Glime 2013b). In the old-growth forest, where competition occurs at the scale of hundreds of years, both strategies are successful. However, the k-strategists have the competitive advantage in the long term, and their ability to influence their own microclimate may be a key factor.

Climate predictions for the PNW suggest there will be hotter summers and wetter winters (US Fish and Wildlife 2011). Epiphytes might be imperative to absorb some of the extra precipitation and provide thermal insulation for host trees against rising temperatures. The type of relationship between epiphytes and microclimates is likely dependent on species and macroclimate; however, in old-growth forests of the PNW, where bryophytes are ubiquitous, bryophyte influence on the microclimate is probable. Having a secondary contributor to microclimate maintenance suggests that the microclimates in the old-growth forest would have a greater resiliency in the face of climate change. Both macro- and mesovegetation (trees and bryophytes) could cultivate microclimates to harbor temperature or desiccation-sensitive species. Understanding the contributors of microclimate development are critical to the management and maintenance of said microclimate.

CONCLUSION

The relationship between microclimates and their associated species is important to consider. The adage that climate drives vegetation has been revised to acknowledge a feedback between vegetation and climate (Hayden 1998). The statement can be further specified to acknowledge a feedback between smaller vegetative structures and microclimates (Stuntz et al. 2002). The epiphytes along the vertical transect of a forest have been characterized extensively and related to microclimatic conditions; however, few studies have addressed how the species interact with the microclimate. The importance of water in climates is imperative to this reframed question as the different species and growth forms of moss differentially hold water based on their structure. Microclimate is tied to structure on both sides of the equation. Microclimates often are assumed to be the product of forest structure, such as tree boles, branch architecture and leaf orientation. However, the influence of epiphytes influencing microclimate is harder to address. Epiphytes are localized structures within greater microclimates, and as such are likely to be critical to the temperature and hydrologic regimes of the microclimate. By characterizing and classifying the relationship between epiphytes and microclimates further, microclimate management becomes easier. Old-growth forests cannot be cultivated to combat climate change, but features of old-growth forests, such as high bryophyte biomass, can be.

This thesis will explore the relationship between bryophytes and microclimates. Chapter 2 explores the dynamic canopy partitioning that creates microclimate zones in the forest. Chapter 3 will focus on the water retention capacity of the four aforementioned epiphytic bryophytes. Chapter 4 brings together these two topics into a conceptual framework to explore how bryophytes might be interacting with their microclimate.

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Chapter 2: Canopy microclimate partitioning in an old-growth Douglas-fir tree at the H.J. Andrews Experimental Forest

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ABSTRACT

Microclimates vary above, below and within the canopy, resulting in canopy zones that can be coupled or decoupled from other canopy zones. The upper, middle and lower canopy zones were classified by their distinct temperature and hydrologic regimes. To determine how the canopy couples and decouples throughout the year, temperature and wetness data from a Douglas-fir, instrumented approximately every 10 m, were analyzed to determine microclimate zones within the canopy and how they vary seasonally. The canopy zones were determined to be dynamic throughout the year, but the upper canopy (56 m) was consistently distinct from the middle and lower canopy. However, the degree of difference between the upper canopy and the rest of the tree varied with season, being lower in the fall and winter than the spring and summer.

INTRODUCTION

Climate conditions below forest canopies are not always coupled with those above (Didham and Ewers 2014), and climate models use satellite data to model vegetative surfaces at the canopy level, rather than the forest floor (De Frenne and Verheyen 2016). Differing microclimates create environmental niches for a variety of flora, as well as refugia for fauna, particularly during extreme climate conditions (Frey et al 2016; Morelli et al. 2016). In the Pacific Northwest (PNW) an old-growth coastal Douglas-fir (*Pseudotsuga menziesii* var.

menziesii), western hemlock (*Tsuga heterophylla*) forest canopy can reach over 60 meters in height, creating a suite of microclimates from the forest floor to the upper canopy. Not only are light levels highly variable (Szaryniski and Anhuf 2001), but relative humidity, temperature, leaf wetness and wind speed are all affected by the height gradient within the forest (Motzer 2005, Rambo and North 2008, Vanwalleghem and Meentemeyer 2009, Didham and Ewers 2014). The decoupling of the upper canopy from the lower canopy is evident in the transition from bryophytes to lichens and the relative abundances of each (McCune 1993, Taylor and Burns 2016, Pypker et al. 2016). Epiphytic lichens dominate in brighter, drier and more variable conditions that are often found in the upper canopy, whereas epiphytic bryophytes succeed in environments that are darker, damper and more stable (Gauslaa 2014), indicating that the upper canopy has a distinct temperature and hydrologic climate regime. A decoupled canopy is defined as a zone of the canopy having a distinct microclimate from other zones.

With lichens being found in the upper canopy, where the microclimate is more variable, and bryophytes found in the middle and lower canopy, it is likely that the mid and sub canopy experience more stable conditions than the upper canopy. In this study, upper canopy is defined as above 40 meters where the foliage is primarily from the dominant trees; the middle canopy is located between 20-40 meters where there is more and evenly distributed foliage from co-dominant trees like western hemlocks and western redcedars; the lower canopy is below 20 meters and reaches the forest floor where most of the foliage is sparse or from understory plants.

These designations are approximate and shift with seasons. However, the microclimate patterns are not as straightforward as the bryophyte-lichen distribution implies. Forest canopy microclimates are influenced by water vapor amount (Vanwalleghem and Meentenmeyer 2009). Large amounts of vapor in the system increase the enthalpy, and subsequently the resistance to rapid air temperature fluctuations (Jones 1992). More importantly, liquid water (4.2 J g^{-1} K^{-1}) has a much higher specific heat capacity than does air (1 J g^{-1} K^{-1}). Therefore, large volumes of canopy water stored in epiphyte mats, leaves, branches, and stems will buffer temperature changes compared to a canopy with lower water content (Jones 1992, Hayden 1998, Lindo and Winchester 2013). The persistence of water vapor also follows the same vertical gradient as the epiphytes (Magrach and Santamaría 2013), being most persistent in the mid and lower canopy. Therefore, not only is the microclimate stability seasonal, but it is influenced by height, suggesting that in the PNW canopy zones may be hydrologically seasonally decoupled.

Temperature and relative humidity are commonly used as proxies for understanding the more complex aspects of canopy microclimates (Szarynski and Anhuf 2001, Heithecker and Halpern 2007, Rambo and North 2008). However, only lichens have been documented as having the ability to absorb water vapor (Lange et al. 2001). Bryophytes must rely on precipitation and dew formation, which can occur when the surface temperature is equal to or lower than the dewpoint temperature and the air is close to saturation vapor pressure (Jones 1992). Canopy surface temperatures register larger amplitudes than air temperatures (Kim et al. 2016), and at night, the radiative cooling in the canopy brings surface temperatures down to dew point, while the air temperature remains too high for dew formation (personal communication).

To explore the duration and influence of water on canopy microclimate profiles, we used data from an old-growth Douglas-fir tree instrumented vertically with multiple high-resolution microclimate sensors to address two hypotheses. 1) The upper canopy experiences more variation in microclimate on a daily scale than the middle and lower canopy. Support of this hypothesis will be shown in the daily data range being greater in the upper canopy than in the lower canopy for temperature, leaf wetness, and relative humidity. 2) The degree of divergence between and among the upper, middle and lower canopy is seasonally dependent. Support of this hypothesis will be shown by comparing the seasonal values of canopy zones for temperature, leaf wetness and relative humidity.

METHODS

Study site

The study site, at the HJ Andrews Experimental Forest (HJA) is located in the Cascade Range of Oregon 44.2122158 N, -122.2552458 W) at approximately 430 m elevation. Summers are warm and dry whereas winters are cool and wet; the HJA receives an average of 2300 mm of rain per year, most falling between October and May (Pypker et al 2006). The forest is characterized by dominant Douglas-fir trees with western hemlock (*Tsuga heterophylla*) and western redcedar (*Thuja plicata*) as the other canopy species. The understory is dominated by vine maple (*Acer circinatum*) and *Vaccinium* spp., as well as sword fern (*Polystichum munitum*) and salal (*Gaultheria shallon*). An important component from the canopy down to the understory is the prolific abundance of bryophytes and lichens (Jonsson 1996). The research was conducted on the Discovery Tree, an individual Douglas-fir in a stand in which the oldest individuals are estimated to be about 500 years old.

Canopy profile measurements

An array of microclimate stations were installed throughout the canopy of the Discovery Tree at heights of 1.5, 10, 20, 30, 40 and 56 m above the forest floor (Figure 2.1). The 56 meter station was place at the highest point safely accessible in the tree, 7 meters from the top. Leaf wetness sensors (LWS, Decagon, Pullman, WA) were installed at all six heights. Temperature sensors (107 thermistor, Campbell Scientific, Logan, UT) are positioned at 10, 20, 30 and 40 meters; the 1.5 and 56 m stations have temperature and relative humidity sensors (HC2S3-L, Campbell Scientific, Logan, UT) and two-dimensional sonic anemometers (Vaisala WAS425A) that record wind direction and speed. Fan aspirated radiation shields were built using the design of Thomas and Smoot (2013) to house the temperature sensors (107 and HC2S3-L models) to minimize radiation bias on air temperature measurements. Data loggers (CR1000 and CR23X, Campbell Scientific, Logan, UT) recorded values every 5 minutes, with each recorded value being the average of the values taken every 15 seconds.

Data Analysis

Data were analyzed for the period from 2 August 2016 to 31 July 2017. Missing data are documented in the appendix.

Using R, basic summary statistics for August, November, February and May for all available sensors were generated to provide a general overview of the seasonality of the Discovery Tree (Figure 2.2, Table 2.1, 2.2). Summary statistics were taken from an average day, created by averaging each 5-minute record across all days of the month for August, November, February and May.

Temperature and leaf wetness were analyzed with time series cluster analysis to explore potential differences among the microclimate stations for four representative months (August, November, February and May). This analysis used a k-Shape agglomerative, complete-linkage clustering and shape-based distance (sbd), a distance measure developed by Paparrizos and Gravano (2015), to create three groupings from the entire time series for each month (dtwclust package in R, Sardá-Espinosa 2017). Three clusters were identified so that each cluster could correspond to a low, middle and upper canopy zone. The shape-based distance between groups was used to determine how closely different microclimate stations patterns correlated to one another. Every valid 5-minute leaf wetness data point for each of the four months was used as a sample unit for each microclimate station.

The time-series cluster analysis was not sensitive to the differences in temperature among height because the strong circadian rhythm of temperature overwhelmed the differences among microclimate stations that occurred at the temperature peaks. Therefore, the temperature data were also analyzed using a generalized additive model (GAM). For each day, the data were aggregated to daily range values, the difference between each daily maximum and minimum temperature, which were modeled using a GAM (mcgv package in R, Wood 2006) with height and smoothed Julian day as the model terms; the model was in the Gaussian family with an identity link. The temperature range data were transformed with a square root transformation due to a moderate right skew to the distribution.

To ascertain seasonal patterns of temperature decoupling in the canopy, the range data were also modeled with the GAM replacing height with seasons, defined as summer (June, July, and August), fall (September, October, and November), winter (December, January, and February) and spring (March, April, and May). All other specifications of the model remained the same including the temperature transformation.

RESULTS

Summary Statistics

In all months, the mean temperature was highest at the top of the canopy with progressively cooler temperatures toward the forest floor. The maximum temperatures followed a similar pattern, except in May, where 40 m had the highest temperature (Table 2.1, Figure 2.2.). Minimum values were similar within each month with no strong vertical pattern. The range was greatest in the upper canopy for all months, but there is not a clear pattern among the other heights.

The leaf wetness data showed that 1.5 meters tends to be the most consistently wet, followed by either 20 or 30 meters (Table 2.2, Figure 2.2). There was a drop in wetness at 10 meters for February and May (data unavailable for August and November). The 56 m station registered the values slightly above 10 m for February and May, but lower in November. November was consistently wet at 10 m, having a minimum value of 532.8 mV. During August, there was no observable surface wetness throughout the canopy except for a few incidences of condensation at night, reaching a maximum of 329.3 mV (Supplemental Figure 2.1), indicating that the upper canopy is the wettest canopy zone in August.

In November and February, relative humidity at the 1.5 m station stayed consistently at 99% with only a few divergences (Figure 2.2). The 56 m station also maintained a high relative humidity during those months, but had more variability. In August and May, the drier months, 56 m experienced lower average relative humidity and a wider inner quartile range.

Time series clustering

Leaf wetness time series clustering showed differences among canopy heights; however, these differences decreased in the winter, revealing a seasonal influence. The 56m (top) and the 1.5m (bottom) station data were distinct from the other stations within the leaf wetness cluster (Figure 2.3). The middle heights, 20 and 30 m tended to cluster together with very low distances between the two while 10 and 40 m changed groups seasonally (Figure 2.3). The greatest difference for leaf wetness occurred in November (0.802 sbd; sbd ranges from 0-2 with 0 being identical and 2 being distinct). The temperature time series are more similar across canopy heights than the leaf wetness. The maximum distance between any two groups was 0.068 sbd, a magnitude smaller than the distances for leaf wetness; this low difference is likely due to the power of the circadian rhythm overwhelming the differences of the temperature peaks and troughs. The greatest separation for temperature still amounts to little to no difference among the canopy profiles; the program requires a predetermined number of groups and therefore the distance between groups is more informative than the actual group designation. The temperature profiles are essentially identical even if the amplitude of daily variation increases with height.

While the shape based clustering minimizes the effects of temporal autocorrelation, the problem of spatial autocorrelation is harder to address. The shape based distance measurements reveal that the spatial autocorrelation might not be a problem for the leaf wetness sensors because distinct clusters were identified in some seasons. However, given that the shape-based distance ranges from 0-2, it is unknown whether the differences among the canopy profiles are being subdued due to spatial autocorrelation.

Generalized Additive Model

The GAM (Eqn. 1) detected differences by height within the canopy profiles by analyzing the daily range of temperature at each microclimate station. The best fitting GAM modeled the square root of the daily range of temperature using height (df = 5) as a parametric coefficient and Julian day (df = 326) as a smoothing term.

Equation 1: $T_{\sqrt{\text{range}}} = f_{(\text{height})} + f\text{s}_{(\text{Julian day})}$

The R^2 was 0.983 and the restricted maximum likelihood (REML) score was -96.8. The Wald test for the model marked all heights as a significant parameter ($p < 0.01$) (Figure 2.4).

The best GAM ($R^2 = 0.959$) to test daily temperature range employed season as a parametric coefficient (df= 3), and Julian day as a smoothing term (df = 326) (Eqn 2); the REML score was 611.68. The Wald test identified summer ($t = 2.238$, $p = 0.254$) and winter ($t = 6.208$, $p < 0.001$) as significant factors (Figure 2.5).

Equation 2: $T_{\sqrt{\text{range}}} = f_{(\text{season})} + fs_{(\text{Julian day})}$

When height and season are modeled together, the patterns identified by individual comparisons persist.

DISCUSSION

Our first hypothesis, that the upper canopy experienced more variation was confirmed. The upper canopy of the Discovery Tree is subjected to a different temperature and hydrologic regime than the mid and sub canopy. It is exposed to direct sunlight, wind shear, and drought (Rambo and North 2008, Taylor and Burns 2016). The mid and sub canopies are shady, have calm winds and reduced water stress. The structure of the forest does not change dramatically throughout the year, with deciduous plants being found in the understory, but the availability of water in the system is seasonal in the PNW. Water availability influences the partitioning of the canopy microclimates, collapsing temperature gradients while exacerbating hydrologic differences when abundant (February) and increasing temperature gradients while collapsing hydrologic patterns when scarce (August, May). While it is worth noting that the year for which data were collected was wetter than average at the HJ Andrews receiving, 112% of average annual rainfall (Daly et al 2009), the annual pattern from wet to dry is still present; however, the total and sustained wetness is possibly exacerbated.

In August, when there was consistent drought, the leaf wetness sensors for all but the 56 and 40 m station consistently read as dry. At the lower heights (10-30 m), surface temperature never reach below dew point and the mid and sub canopies stayed dry. A few days in August

2016, and again in May, June and July 2017, the top of the canopy reached surface temperatures low enough to incite condensation (Supplemental Figure 2.1). In August, the top of the canopy recorded 329.3 MV, or ~33 g/m^2, of water condensation, while the rest of the canopy remained dry. A similar phenomenon happened at 40 m, but to a lesser degree. The occurrence of condensation at the top of the Discovery Tree makes the top of the canopy more variable than the lower canopy during dry months. During the wetter months, considered to be November through April (Daly et al. 2010), the top of the canopy is dryer than the lower canopy. While August, November and May all have a greater variation in average daily wetness (Figure 2.2b), February presents a very narrow upper canopy range. This finding could be due to consistent cloud cover keeping a fine layer of moisture on the canopy, the low solar angle of the sun reducing the amount of radiation reaching the valley, or reduced wind speeds in the upper canopy due to cold air pooling in the lower canopy (Pypker et al. 2007b); however, more exploration is necessary. The usual variation in the upper canopy is likely due to interactions with wind speed, which is usually greater at the top of the canopy (Supplemental Figure 2.2). It is worth noting that for the entire month of November, the wetness sensor minimum for 1.5 and 10 m read as 383.2 mV (53.4 g/m^2) and 409.8 mV (67.3 g/m^2) of water, indicating that the surfaces at these heights were consistently wet throughout the entire month. The average daily minimum for February and November also showed consistent wetness (Table 2.2)

Temperature variability was also greatest at the top of the canopy, with a steady increase from the lower canopy upwards.). The GAM confirmed that the temperature regime of the canopy is distinct for each microclimate station (Figure 2.4), but that this separation is minimized in the winter and exacerbated in the summer (Figure 2.5). When looking at a typical day, the circadian pattern of the 1.5 meter is nested inside the 10 m, which falls inside the 20 and so on.

The upper canopy at 56 m reaches hotter temperatures during the day but returns to roughly the same minimum at night as the rest of the canopy. The significance of height in the GAM model is expected, as height is a conglomerate of environmental factors (canopy cover, vegetation and density). The amount of temperature fluctuation per day is correlated with water availability, in that the drier days/months have higher ranges than wetter days/months. This pattern is likely due to fluctuations and solar radiation and the high heat capacity of water, absorbing and releasing heat as temperatures fluctuate, stabilizing the environment when present (Hayden 1998).

The leaf wetness cluster analyses revealed consistent decoupling of the upper canopy from the mid and lower canopy, but like temperature the degree of separation among the clusters is seasonal. The upper canopy was hydrologically decoupled from the rest of the tree in every month analyzed with cluster analysis. The intermittent nightly spikes create two main clusters in August: 56 m and 10-40 meters. Of the months analyzed, November had the greatest difference in time-series clustering. Due to consistent wetness in the lower canopy, the separation for November between the upper canopy (56 and 40 m) is likely due to the effect of winds wicking water off the surface and effectively drying out the canopy. In February, the upper canopy still separates itself from its closest neighbors, but 1.5 m has the greatest separation. The consistent wetness of the lower canopy marks it as decoupled from the atmosphere to a greater extent than the upper canopy.

August is notably the least different among the heights of the tree, having a maximum distance 0.48; this minimal difference is likely due to the consistent dryness of the summer with the top of the canopy breaking out due to the condensation in the upper canopy. However, the condensation reactions were not consistent or long enough to produce a large difference. The other microclimate stations in August have a maximum distance of 0.08, implying that they experience the same hydrologic microclimate.

CONCLUSION

With both hydrologic and temperature decoupling, the upper canopy was determined to experience a much different microclimate than that of the lower and middle canopy. However, the lower canopy also has distinct decoupling in the wettest months. As the strength of temperature separation among microclimate stations decreases, the strength of hydrologic separation increases so that the upper canopy is consistently decoupled from the lower canopy, but due to different microclimate variables. The implications of these findings are both practical and ecological. Models based on satellite imagery need to consider layered microclimates in modeling predictions of temperature and climate change. Ecologically speaking, climate refugia are becoming increasingly important to organisms (Frey et al 2016), and preserving forests that can decouple atmospheric warming from ground warming may be critical for species survival. The dynamic nature of microclimates and canopy decoupling makes their continued exploration imperative in the age of climate change.

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Figure 2.1: Discovery Tree Schematic

Location of microclimate stations, each having a temperature and leaf wetness sensor, within the Discovery Tree. Exclosures containing data loggers are at 1.5 and 56 meters. (Drawing from Van Pelt and Nadkarni 2004).

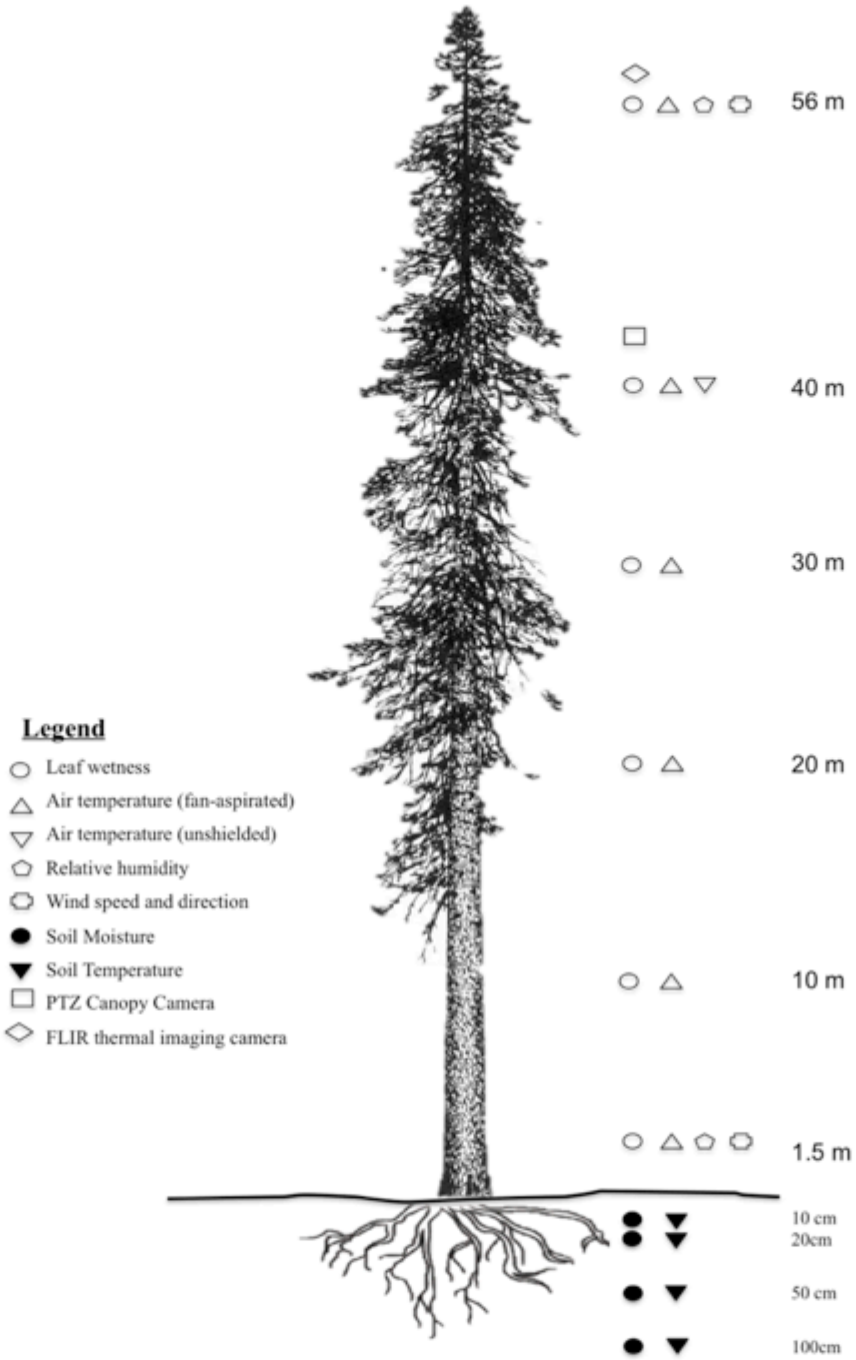


Figure 2.2: Climate data distributions for 56 and 1.5 m

For 56 and 1.5 m, the distribution of temperature (A), leaf wetness (B) and relative humidity (C) data for each month is plotted. The data are aggregated by month and only spurious data points were removed. Wetness was unavailable at 1.5 m in August; wetness values range from 265 (dry) to 1000 (completely wet).

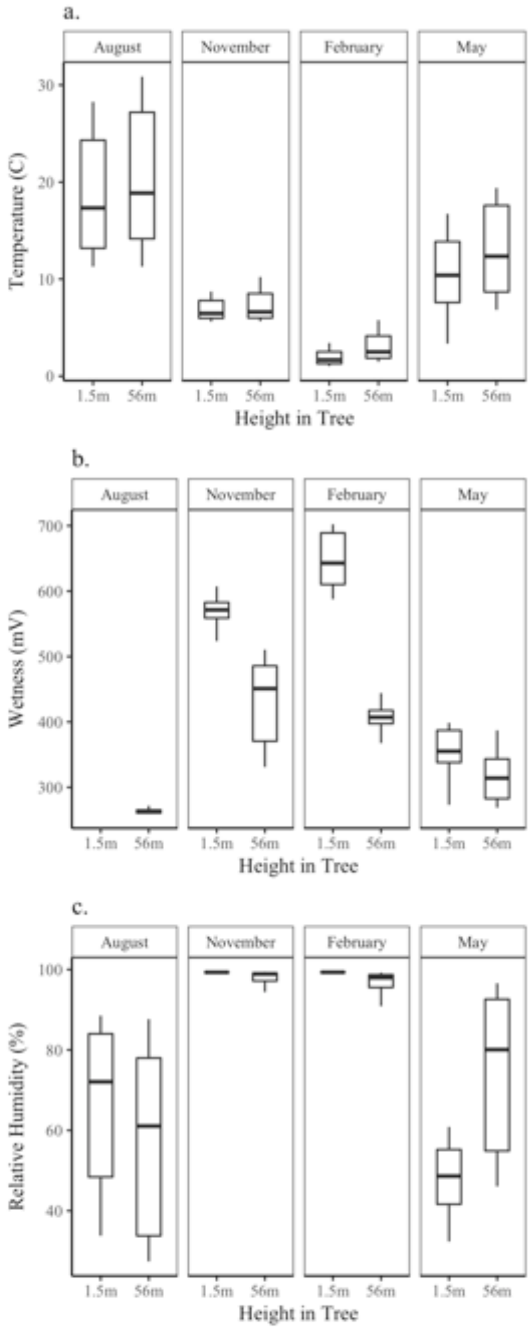


Figure 2.3: Cluster Analysis Diagrams

Leaf wetness time-series clustering for four months (August, November, January and March); distance represents dissimilarity between different microclimate profiles; longer arms indicate greater dissimilarity. The label color indicates canopy zones (red = upper canopy, blue = middle canopy, black = lower canopy). Shape-based distance ranges from 0-2.

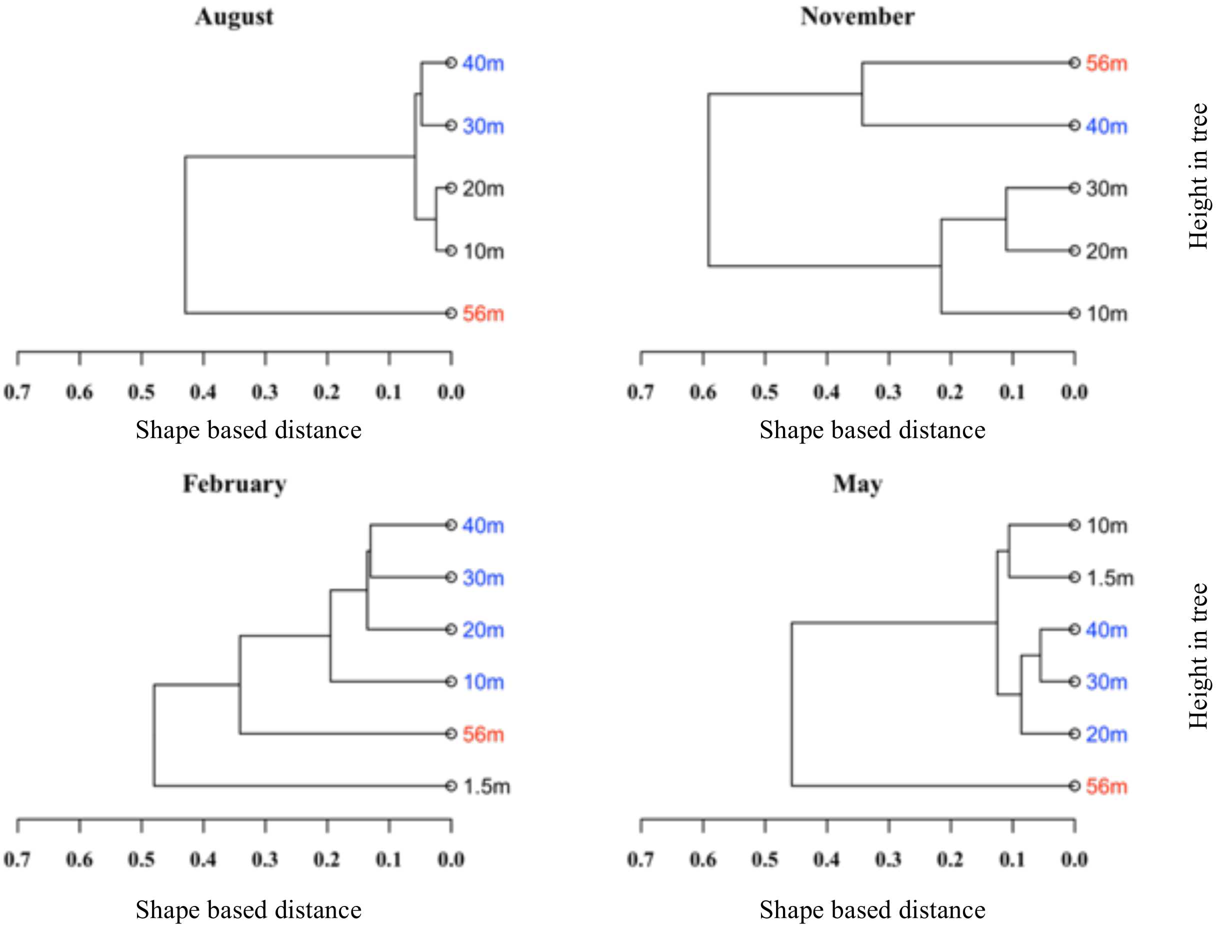


Figure 2.4: Daily temperature range GAM estimate by height

The daily temperature range, calculated for every day from 2 August 2016 to 31 July 2017, at each height was found to be significantly different from every other height. The plot displays the model's mean temperature range estimate and confidence interval.

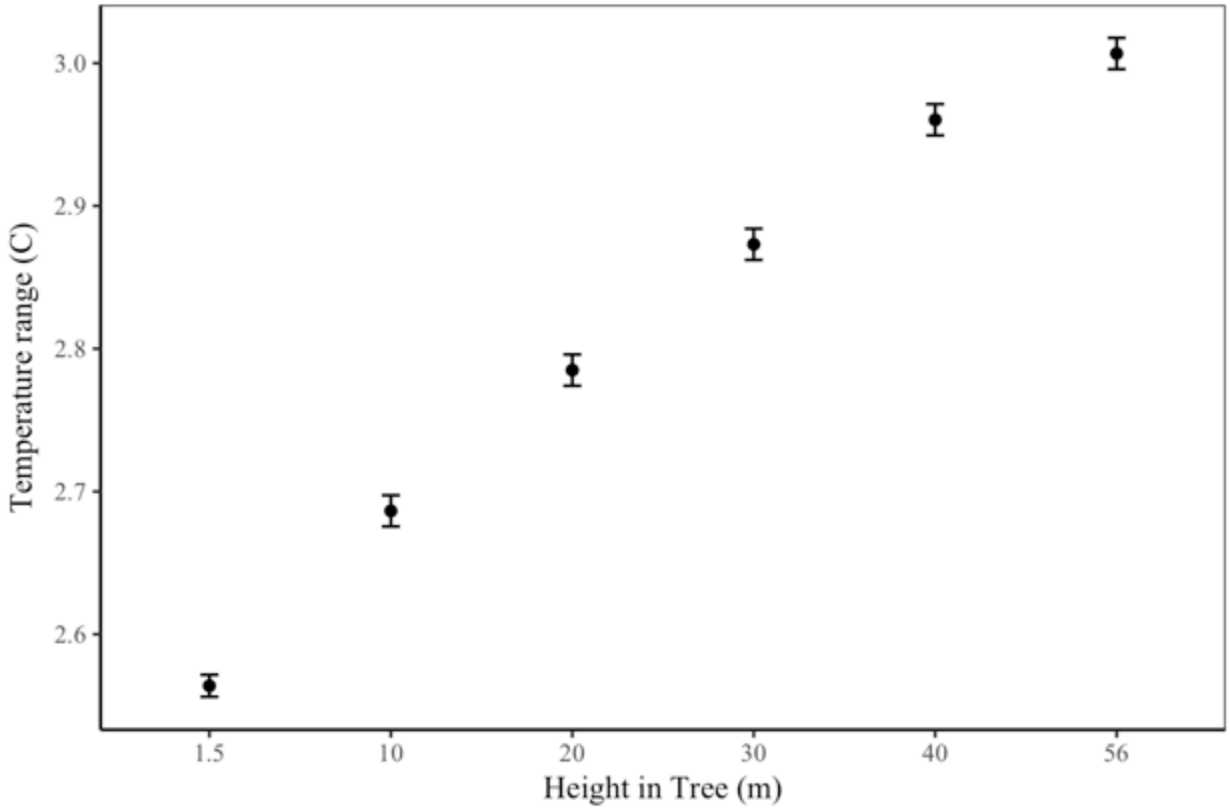


Figure 2.1: Temperature range GAM estimate by season

The daily temperature range, calculated for every day from 2 August 2016 to 31 July 2017, varies by season as well. The plot displays the model's mean temperature range estimate and confidence interval.

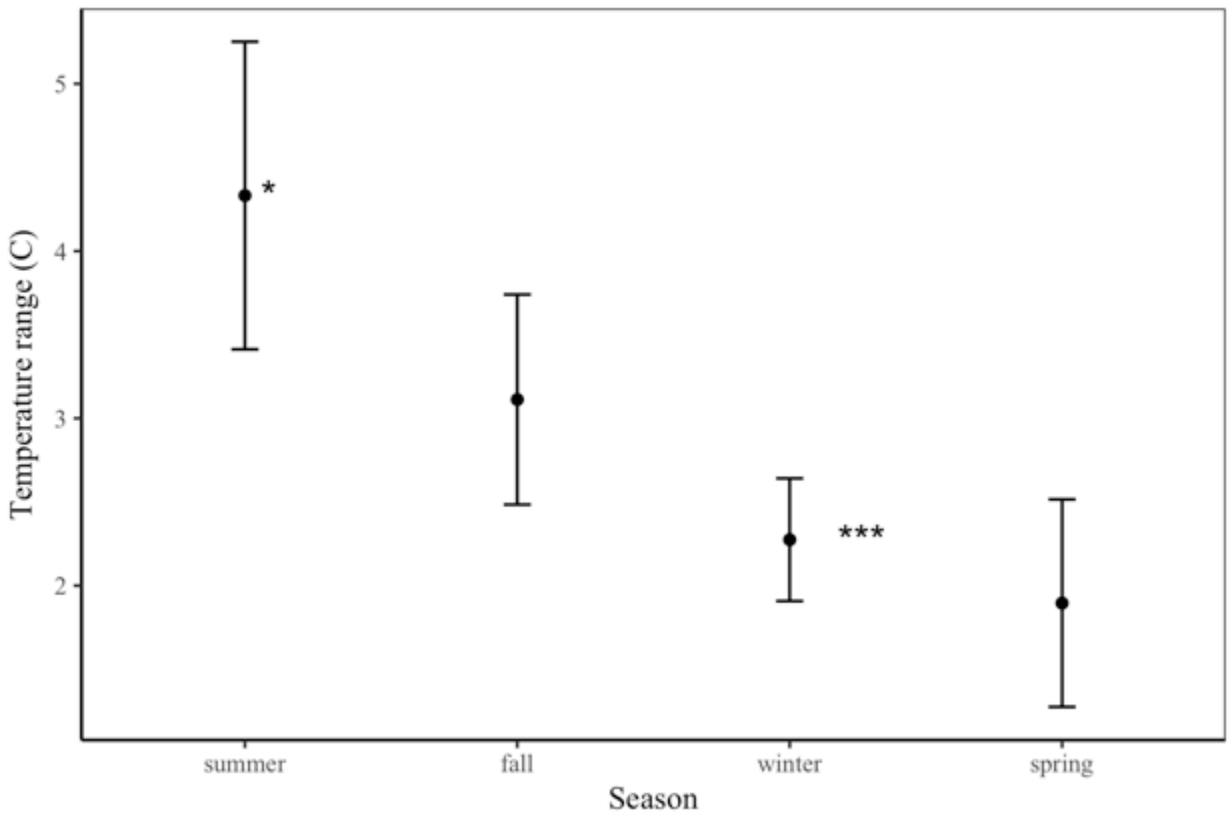


Table 2.1: Temperature Summary Statistics for 4 representative months

Mean temperatures for each month steadily increase as height in the tree increases, and the ranges of each follow suit. The ranges follow a similar pattern to the relative humidity with much wider ranges in drier months. Values are based on an average day for each month, which was aggregated by time for each height.

Microclimate Station	1.5 m	10 m	20 m	30 m	40 m	56 m
August						
Min °C	7.55	7.31	7.22	7.24	7.10	7.14
Mean °C	18.60	19.02	19.28	19.55	19.87	20.30
Max °C	35.33	36.96	37.58	38.51	41.57	42.52
Range °C	27.79	29.65	30.36	31.28	34.47	35.38
November						
Min °C	0.72	0.45	0.29	0.32	0.33	0.41
Mean °C	6.85	6.74	6.77	6.92	7.01	7.28
Max °C	13.24	13.66	14.16	16.78	16.18	17.41
Range °C	12.52	13.21	13.87	16.46	15.85	17.00
February						
Min °C	-1.07	-1.35	-1.48	-1.49	-1.56	-1.56
Mean °C	1.94	2.19	2.42	2.63	2.79	3.07
Max °C	7.72	8.72	9.55	11.19	11.85	13.63
Range °C	8.79	10.07	11.03	12.68	13.41	15.19
May						
Min °C	0.26	-0.04	-0.19	-0.07	-0.12	0.01
Mean °C	10.94	12.27	12.45	12.71	12.87	13.00
Max °C	30.80	32.37	32.70	33.22	33.70	33.44
Range °C	30.54	32.41	32.89	33.29	33.82	33.44

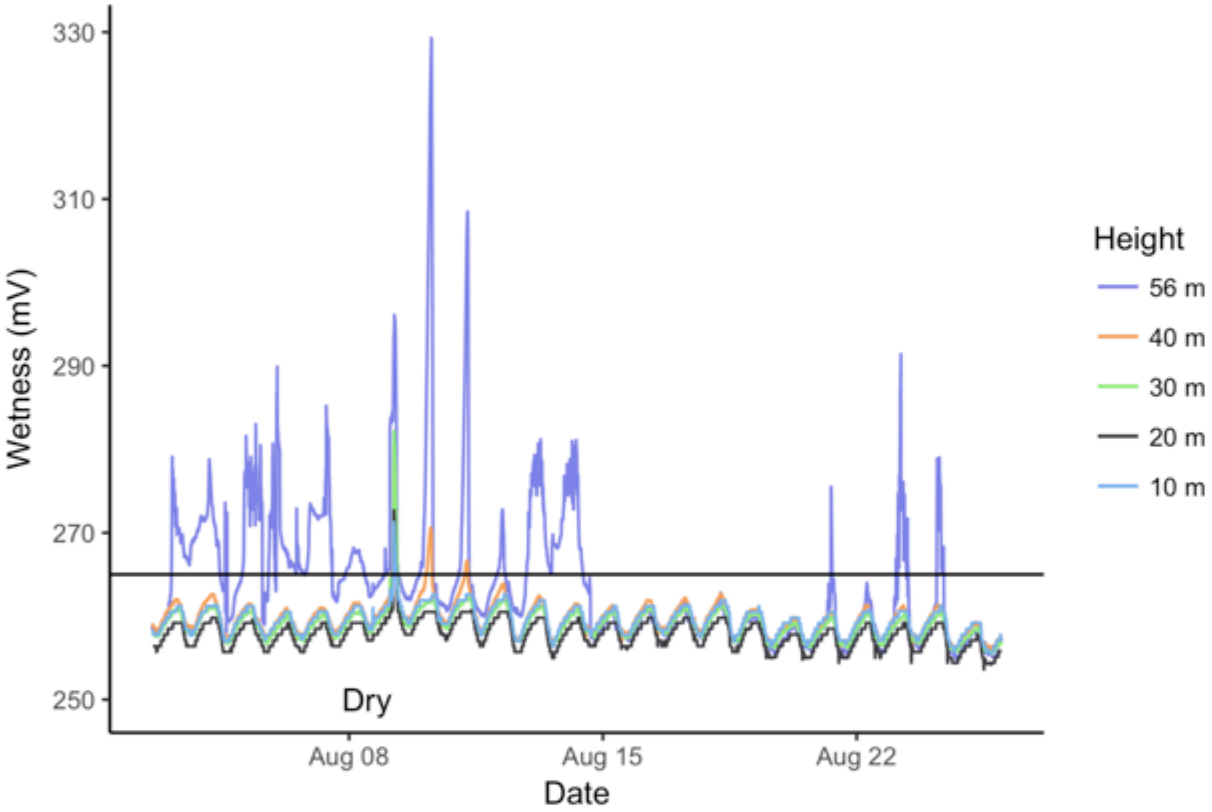
Table 2.2: Wetness Summary Statistics for 4 representative months

Wetness fluctuates most in the wet months, and particularly when there are freezing events. August stayed consistently dry at all heights except for the upper canopy which experience periodic, ephemeral wetting. Notably, the lower canopy, 10 m stayed wet for the entire month of November; 1.5 m in November was only installed on November 14th, and therefore remained consistently wet for the second half of the month. Values are based on an average day for each month, which was aggregated by time for each height. The millivolts (mV) unit is dry below 265 mV and has a maximum value of 1000; the converted g/m^2 is listed with the mV unit, but due to conversion from an exponential function, the dry value for the wetness sensor reads as ~20 g/m^2 and become unreliable after 700 mV.

Microclimate Stations	1.5 m	10 m	20 m	30 m	40 m	56 m
August						
Min mV; g/m^2	NA	259.5; 18.4	257.8; 18.1	259; 18.3	259.8; 18.4	263.8; 19.0
Mean mV; g/m^2	NA	257.5; 18.0	255.9; 17.8	257.2; 18.0	257.5; 18.0	259.5; 18.4
Max mV; g/m^2	NA	261.4; 18.7	259.8; 18.4	261.3; 18.6	262.9; 18.0	272.9; 20.6
Range mV; g/m^2	NA	3.9; 2.0	3.9; 2.0	4.1; 2.0	5.4; 2.0	13.4; 2.2
November						
Min mV; g/m^2	570.3; 269.1	532.8; 194.7	542.9; 212.4	489.6; 134.0	417.2; 71.7	433.0; 82.2
Mean mV; g/m^2	523.6; 179.8	518.0; 171.3	516.0; 168.4	455.1; 99.5	344.1; 38.1	331.0; 34.0
Max mV; g/m^2	607.3; 370.5	548.4; 222.7	567.7; 263.2	520.2; 174.6	474.9; 118.0	510.4; 160.4
Range mV; g/m^2	83.7; 4.0	30.4; 2.5	51.7; 3.0	65.1; 3.4	130.8; 6.0	179.4; 9.2
February						
Min mV; g/m^2	647.4; 523.9	354.4; 41.7	449.7; 94.9	492; 136.8	484.9; 128.7	406.5; 65.4
Mean mV; g/m^2	587.7; 312.8	342.4; 37.6	419.8; 73.3	458.4; 102.4	448.2; 93.7	361; 44.1
Max mV; g/m^2	702.3; 841.9	363.4; 45.0	483.5; 127.1	542.9; 212.4	545.3; 216.9	462.8; 106.3
Range mV; g/m^2	114.6; 5.2	21; 2.3	63.7; 3.4	84.5; 4.0	97.1; 4.5	101.8; 4.7
May						
Min mV; g/m^2	360.8; 44.0	295.5; 25.1	330.5; 33.9	308.3; 28.0	321.6; 31.4	314.2; 29.4
Mean mV; g/m^2	273.2 20.7	235.3; 14.9	282; 22.3	288.2; 23.5	295.6; 25.1	268.8; 19.9
Max mV; g/m^2	398.6; 61.1	318.9; 30.7	373.7; 49.2	326; 32.6	353; 41.2	387.1; 55.3
Range mV; g/m^2	125.4; 5.8	83.6; 4.0	91.7; 4.3	37.8; 2.7	57.4; 3.2	118.3; 5.4

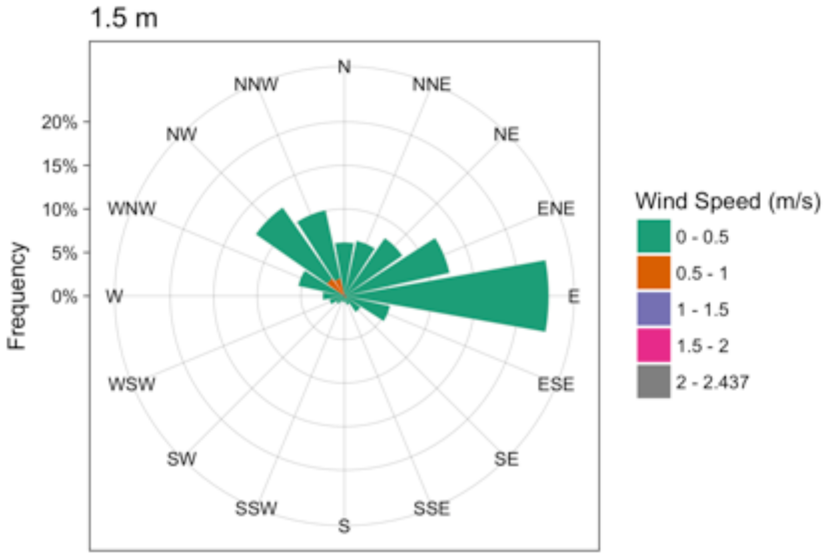
Supplemental Figure 3.1: August Wetness

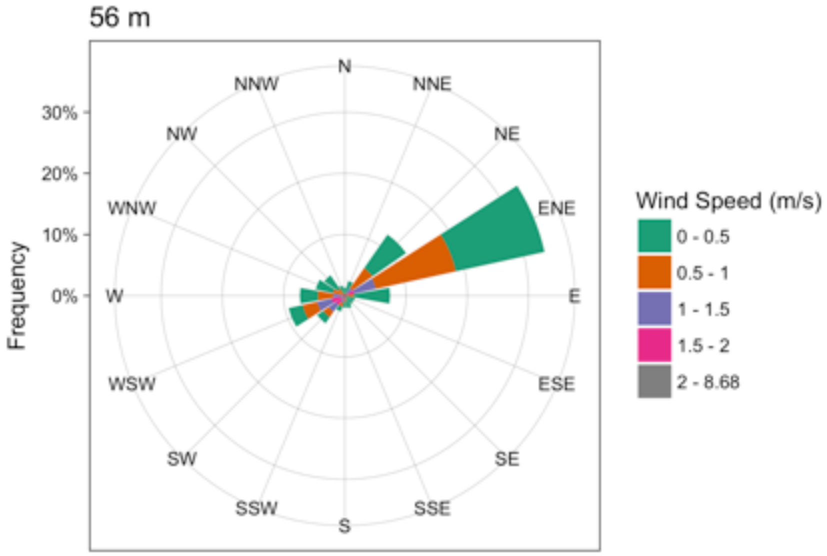
Demonstrating the intermittent wetness that occurred at the top of the canopy in the summer (observed in August 2016, May, June and July in 2017). Surface temperatures at 56 m reached dew point, even when air temperatures do not, causing a condensation reaction. The phenomenon occasionally reached 40 m, but it was much less common.



Supplemental Figure 3.2: Wind speed and direction at 1.5 and 56 m

The upper canopy has consistently higher wind speeds than the lower canopy. Additionally, the lower canopy appears to have been buffeted, as there is a greater distribution of wind directions in the lower canopy. The size of the bar indicates frequency of wind coming from the direction on the compass.





Chapter 3: Watching moss dry: Assessing the water retention capacity of four canopy bryophytes

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ABSTRACT

Old growth Douglas-fir (*Pseudotsuga mensezii)* and western hemlock (*Tsuga heterophylla*) forests are known for their heavy epiphyte loads. The relationship between epiphytes and microclimate can be directional, in which microclimate drives epiphyte populations, or interactive, in which microclimate and epiphytes interact in a potential feedback loop. Water not only retains heat but can also cool during evaporative heat loss, and the ability for an epiphyte to hold water for longer time periods influences the nature of the relationship. This study investigated the ability of four genera of bryophytes to retain water from 20 and 60 mm "rain" events in the greenhouse. The four species selected, *Neckera douglasii, Porella navicularis, Isothecium stoloniferum* and *Dicranum fuscescens*, are commonly found in old-growth forests in the Pacific Northwest. Each species was sprayed with water and measured for changes in mass every hour for the first day and then subsequently three times a day to monitor water loss. Slower-growing taxa, *Neckera* and *Dicranum*, retained water for 4.5 days after a 60 mm rain event, while the faster-growing taxa, *Isothecium* and *Porella*, retained water for only 3 days. These results suggest that while all of four genera can be found in both second and old-growth forests, the longer water retention time for *Neckera* and *Dicranum* is likely to amplify their influence on microclimate in old-growth forest trees. To further gauge the influence of these differences in water retention times in the field, the distribution of epiphytic bryophytes was also assessed on a ~300 year old Douglas fir (*Pseudotsuga menziesii*). We estimated epiphyte biomass visually in 1 m bands at microclimate stations and including all branches attached in those bands at six vertically arrayed heights within the tree (1.5, 10, 20, 30, 40 and 56 m above ground). We used a calibrated visual index to estimate biomass. The total bryophyte biomass was greatest at 30 meters and decreased at microclimate stations above and below that point, but with a slight increase at the 1.5 m station. The old-growth associates and second growth associates were found throughout the canopy. Taken together, these results suggest the importance of knowing the species-specific bryophyte water retention capacity and its height distribution to better understand how the species functions thermally and hydraulically within the canopy.

INTRODUCTION

Moss is ubiquitous in the Pacific Northwest (PNW) old-growth forests. These forests also experience heavy rainfall from October until April (Jonsson 1996). While high rainfall is not an obligate condition for moss, the abundance and sheer amount of this type of vegetation is enhanced by frequent rain events. Mosses and liverworts (hereafter referred to as the paraphyletic group known as “bryophytes”) are poikilohydric, meaning they are able to desiccate and remain dormant until conditions suitable for photosynthesis arise (Kimmerer 2003, Batke et al. 2015). Thus, water retention is of paramount importance to these organisms. Epiphytic bryophytes are even more susceptible to desiccation, as they are not sheltered from dehydrating forces, such as light and wind (Batke et al. 2015).

Second growth forests have a much lower epiphyte load compared to old-growth forests (Price et al. 2013). In old-growth forests, the contribution of bryophytes to canopy water storage is roughly double that of a younger stand with the same leaf area index (Pypker et al. 2006). . Second growth forests in the region may be hotter than old-growth forests , which may be related to their limited epiphyte loads, as increased water retention would lead to faster heating rates (personal communication).

The distribution of epiphytes along a tree can be described by Whittaker's variable density over an environmental gradient, in this case a vertical gradient (Sillet and Rambo 2000). Epiphytes are closely associated with the microclimatic gradients that persist throughout the vertical structure of a tree (Grimbacher and Stork 2007, Batke et al. 2015, Taylor and Burns 2016). McCune et al. (2000) found that height was the strongest predictor of epiphyte community assemblage, followed by host organ (trunk, branch, twig), trunk lean, substrate and host species. With increasing height, light levels (Magrach and Santamaría 2013) and wind speed (Motzer 2005) increase, but other environmental factors are harder to generalize due to seasonal fluctuations. Bryophyte colonization throughout the tree starts at the base and "climbs up" as the tree continues to grow, leaving bryophytes covering most of the lower trunk and branches (McCune 1993, Coxson and Coyle 2003). However, bird and arboreal fauna mediate some species colonization among treetops (McCune et al. 2000). Generally speaking, these distributions patterns reflect lichens dominating treetops and bryophytes preferentially occupying the mid-canopy (~20-40 meters in old-growth Douglas-fir forests) (McCune et al. 1993, Pypker et al. 2006).

This study focused on differential water storage and retention capacities of four common bryophyte genera: *Dicranum, Isothecium, Neckera,* and *Porella*. In an old-growth Douglas-fir ecosystem, these four genera are divided mainly by life-cycle strategy and growth form. While all four are perennial bryophytes, *Isothecium* and *Porella* have a "bet hedging" strategy, while

Neckera and *Dicranum* are identified as K strategists (Glime 2013a). Bet hedging is a middle strategy where species are proficient at both sexual and vegetative reproduction, but may be outcompeted in an environment that is extremely stable, such as an old-growth forest. A K-strategist, such as *Neckera* or *Dicranum*, is able to slowly dominate the canopy, growing over the other bryophytes as it capitalizes on the ecosystem. The designation of *Neckera* and *Dicranum*, and *Porella* and *Isothecium*, as K-selected or bet hedging is not to be interpreted as an absolute (Glime 2013). On the spectrum from r to K strategists, the four species fall closer to the perennial, stable model; however, certain characteristics separate the two groups enough to adopt these terms.

These growth form differences underscore life-cycle strategies. Bryophyte structure and growth form affect water retention (Vilde 1991). *Dicranum* is defined as a tall-turf, which is able to maximize water storage and move water internally due to its hemispheric shape (Glime 2013b). *Porella* and *Neckera* are both identified as fans, a common epiphytic structure; however, these genera differ in their leaf structure. *Porella* is a liverwort with larger, fewer leaves arranged in a sparse branching pattern and forms less dense mats than *Neckera* (personal observation). *Isothecium* is a frequently pendant moss, which has long trailing main stems (Glime 2013). It can grow in a variety of forms, but in this study this taxa was predominantly the pendant form, typically hanging from the branches. The pendant form is well suited to collecting water droplets from clouds and fog (Glime 2013).

The relationship between life-cycle strategy and growth form drives differential water storage capacities. We hypothesize that: 1) The slower-growing taxa *Neckera* and *Porella*, are able to store water for a longer period than the faster-growing *Isothecium* and *Porella* independent of the amount of water intercepted; and 2) The size of the epiphyte mat will have a multiplicative effect on water storage, such that larger mats will store greater amounts of water. Determining the retention rate of water in the system can help to parse out how increased canopy water storage influences directional and interacting relationships of epiphytes and microclimates. The study tree has moderate bryophyte cover on its trunk and limbs; when combined with the climate data collected from the microclimate stations located every 10 m, the tree provides a unique platform to study potential relationships between bryophytes and microclimates.

METHODS

Experimental system

The field study was conducted at the HJ Andrews Experimental Forest in the Cascade Range of Oregon (44.2122158 N, -122.2552458 W, 430 m, 2100 mm rainfall). Bryophytes were located on one extensively and intensively instrumented old-growth Douglas-fir (*Pseudotsuga menzeisii* var. *menziesii*) tree, the Discovery Tree, within an approximately 500 year old forest. Microclimate stations were installed on the Discovery Tree at 1.5, 10, 20, 30, 40 and 56 m; each microclimate station has an aspirated temperature sensor (107 Campbell Scientific, Logan, UT, HC2S3-L Campbell Scientific, Logan, UT), and a leaf wetness sensor (LWS Decagon, Pullman, WA) (Chapter 2). The 1.5 and 56 m stations also have relative humidity sensors (HC2S3-L Campbell Scientific, Logan, UT) and wind speed and direction anemometers (05103-L Campbell Scientific, Logan, UT). Finally, the 56 m station also has a thermal camera on a pan-tilt mount. Single rope climbing technique was used to access the microclimate stations. The Discovery tree extends above 56 m; however, it is unsafe to climb above that height.

Primary branch and bryophyte distribution with height

Branch distribution, epiphyte biomass and epiphyte diversity were estimated at each microclimate station. The most common species of epiphytic bryophytes encountered on the height transect were *Dicranum* spp., *Isothecium stolonifera, Neckera douglasii* and *Porella navicularis*; these taxa are the focus of this study. Field estimates did not parse species differences of *Dicranum*, of which there are three possible species that could be found; there is only one possible species for the other three genera. However, taxa will be referred to by their genera throughout.

While climbing, the number of primary branches, defined as those branches attached directly to the trunk, was counted in each height zone: 0-1.5, 1.5-10, 10-20, 20-30, 30-40, and 40-56 m. We estimated the epiphytic bryophyte biomass in the Discovery Tree at 1.5, 10, 20, 30, 40 and 56 m. Estimates were taken from the meter band centered at the microclimate station, 0.5 above and below microclimate stations, and extending to the end of all branches in each band. We visually estimated bryophyte biomass by comparing mats in the tree to photographs, described below. This method follows McCune et al. 2008, who showed that this method was accurate within an order of magnitude for lichen species. At each of the six height locations, we also identified all bryophyte species present to calculate a Shannon diversity index.

Water loss curves for bryophytes in greenhouse

The greenhouse experiments focused on four species of bryophyte: *Dicranum fuscescens, Isothecium stolonifera, Neckera douglasii* and *Porella navicularis*. Because of a prohibition of harvesting epiphytes from the Discovery Tree, we collected plant material that had fallen to the ground in the tree's vicinity and also from two other forests in similar ecological zones: the Willamette National Forest (44.18984,-122.08797, 500 m, 2000 mm precipitation) and the Oregon State University McDonald Research Forest (44.562951,-123.3535766, 175 m, 1700 mm precipitation). Samples were harvested in August and November 2016. The bryophyte material was separated by taxa into three weight classes (1.0, 5.0, and 10.0 g dry weight) with six replicates of each class. Samples were photographed alongside a scale.

We assayed the water retention capacity and rate of water loss of bryophyte samples in the greenhouse. Using the samples described above, we randomly selected three replicates from each taxon and weight class (3 reps of 1.0, 5.0, and 10.0 g dry weight for each taxon). Each replicate's planar area was measured using its major and minor axis, assuming it has the form of an ellipse. The planar area was used to calculate the appropriate water volume to apply to each sample to simulate these rainfall events. Because rainfall in storm events at the HJA clusters around 20 and 60 mL per m^2 ground area (Pypker 2004), these two sizes of rain event were simulated.

We weighed each air-dry sample, applied the appropriate water volume to each sample using a spray bottle, and then recorded sample weight every hour for the first five hours, and then three times a day thereafter (9:00, 13:00, and 17:00) until the sample returned to its original air-dry weight. The 20 mL simulation was repeated four times and the 60 mL simulation was repeated twice; samples were not used more than twice for each simulation. One limitation of the method was that it was difficult to get the samples to absorb the entirety of a rain simulation event. Water that ran through samples immediately upon spraying was collected in a catchment basin and weighed so that the total amount of water added to the sample was accurate. However, this throughfall make it difficult to force consistent volumes of water into each sample; this limitation required proportional mass remaining to be used for analysis to standardize drying curves.

For each drying event, we collected climate data within the greenhouse to help explain the drying curves. A data logger (EM50, Decagon) recorded leaf wetness (LWS, Decagon), temperature, relative humidity, vapor pressure (VP-3, Decagon), and photosynthetically active radiation (PAR) (PAR Sensor, Decagon), recording a measurement from every minute every 15 minutes.

Lastly, we tested sample saturation by submerging them in water for five minutes, allowing them to drip-dry water ten minutes and dabbing off large droplets of water with a paper towel (Köhler et al. 2010). Samples were then weighed to get their water-saturated mass.

Data Analysis

The epiphytic bryophyte distribution data were aggregated to assess total biomass at each microclimate station. Biomass was plotted by height to gauge vertical distribution. Where multiple branches were present, the biomass for each branch was summed. A species richness and Shannon-Weiner index ($H' = -\Sigma\ p_i \ln(p_i)$) were calculated.

To interpolate values between measurements and to incorporate data from replicate dry-downs, we modeled the dry-down curves using exponential decay functions (minpack.lm package in R, Elzhov et al. 2016) of the form: $\beta_1 e^{--\beta 2 * \text{time elapsed}}$. Each separate trial (species, weight, and rain event) was interpolated and the average values of each curve used to generate the final curve. We then ran correlations between the raw data and the fitted models to assess the quality of the models.

The values for β_1 and β_2 were extracted from each model and least square means were calculated to test for differences (lsmeans package in R, Lenth 2017). The intercept, β_1, corresponds to how much water was absorbed for each "rain event," The value of β_2 represents the rate at which the water evaporated. A plot of the samples' intercept value vs. observed water saturation level showed that the 1 g samples dried too quickly to model with an exponential decay, and so we only used the 5 and 10 g samples for interpretation.

We then built models to test for differences between species and weights, treating dry-weight as an additive term for the intercept value (β_1) but as an interaction term for the dry down rate (β_2). The saturated values for the bryophytes were compared to the $\beta_1$values using the least square means values for each weight class.

Because the climatic factors we measured are expected to interact multiplicatively, we used non-parametric multiplicative regression (NPMR) in HyperNiche (McCune 2006, McCune and Mefford 2009) to identify which factors had the strongest influence on the drying rates. Using temperature, relative humidity, and PAR as independent variables, we built a local mean – Gaussian model with a conservative control on overfitting to predict bryophyte drying rates. Models were evaluated based on leave-one-out cross validation (xR^2). The models were run for the 10 g sample under the 60 mm rain simulation, as these models produced the best fitting drying curves ($xR^2 = 0.81$) using a free search with a maximum of 500 trials.

RESULTS

Primary branch and bryophyte distribution with height

Looking at the total biomass at each microclimate station, the greatest proportions of epiphytes are found from 20-40 meters, which corresponds to 16 branches, 5 branches between 20 and 30 m height, and 11 branches between 30 and 40 m height. Most of the biomass (74.7%) was on the branches. The diversity of bryophytes mimics the biomass distribution; the highest Shannon Index was calculated at 30 m (H’ = 1.75).

Estimated biomass at each microclimate station of bryophytes was highest in the zone from about 20 to 40 m in the tree, but the distribution varied by taxon (Figure 3.1a, b). *Porella*, *Neckera*, and *Dicranum* had the highest biomasses in the 20-40 m height range, but *Isothecium* distribution was relatively constant from 1.5 m to 40 m and not detected above that. Two common species were not targets of this study, including *Kindbergia*, a terrestrial bryophyte found mostly at the base of the tree, and *Antitrichia*, which was only found at 30 and 40 m. The total epiphyte distribution did not mirror the number of primary branches from the trunk (Figure 3.1c). The canopy zone from 20 to 40 m in the Discovery tree had more branches than the zone below 20 m, but fewer than the zone above 40 m. The Shannon diversity index (Figure 3.1d) had a similar pattern to the total bryophyte distribution (Figure 3.1a).

Water loss curves

Figure 3.2 shows fitted curves for the 10 g samples to show an example of the shape of the dry-down curves. The model fitting for the water loss curves showed good correlations between actual and modeled data for *Neckera* and *Dicranum* ($R = 0.78$ to 0.88, Table 3.1). The correlations tended to be weaker for *Porella* and *Isothecium* ($R= 0.63$ to 0.86, Table 3.1), but still produced relatively strong correlations.

Only the 1 g sample reached complete saturation (Supplemental Figure 3.1), likely because the larger samples had air trapped within them. However, in the field, and in the canopy in particular, there is likely to be air in the interstitial spaces of the bryophytes and therefore this method as an estimate of saturation capacity should be valid, even if total saturation was not attained (Köhler et al. 2010) (Supplemental Figure 3.1).

The proportion of water absorbed from the rain simulation, (β_1), differed by species (Table 3.2). *Dicranum* had the lowest values, both for the 20-mm and the 60-mm rainfall events.

For both the 20 and 60 mm simulations, *Dicranum* the lowest median intercept, being 3.2 g of water per gram dry mass (gH_20/gdw) for the 60 mm x 10 g simulation and 1.3 gH_20/gdw for the 20mm x 10 g (Table 3.2); for the sake of clarity, the 10 g sample proportions are reported with other proportions present in Figure 3.3. *Neckera* had the highest median starting proportion of water for the 60 mm rainfall events (5.7 gH_20/gdw), but was not distinguished as storing more in the 20 mm simulation (2.7 gH_20/gdw). The *Isothecium* and *Porella* had initial proportions between the *Dicranum* and *Neckera* (4.1 and 5.0 gH_20/gdw respectively) for the 60 mm rainfall events.

In contrast to the pattern with β_1, the rate of drying, (β_2), did not differ significantly among species (Table 3.3). However, whereas the rates were not significantly different, the mosses did differ in their proportion of water remaining after 48 hours in the 60 mm addition experiment (Figure 3.4). After 48 hours, the 10 g sample of the *Neckera* has the highest proportion of water remaining (1.1 gH_20/gdw), followed by *Dicranum* (0.9 gH_20/gdw), then *Porella* (0.6 gH_20/gdw), and *Isothecium* was the driest (0.3 gH_20/gdw). There was no pattern within the 5 gram samples; all genera stored a proportion of ~0.5 gH_20/gdw. The 1 gram sample showed *Isothecium* being best able to store water (0.6 gH_20/gdw), with *Neckera* storing the least (0.1 gH_20/gdw).

The resulting models from NMPR (McCune and Mefford 2009) were graphed on 3D projections and analyzed. Each model used elapsed time as a predictor; other predictors and their weights are listed in Table 3.4. The model for *Neckera* had an xR^2 value of 0.909, with a mean proportion of water of 3.19 (standard deviation = 1.23), indicating that *Neckera* retained water at higher volumes for longer. The *Dicranum* model ($xR^2 = 0.91$) predicted the mean proportion of water remaining for *Dicranum* to be lower than hypothesized, being 2.11 gH_20/gdw (s = 0.88).

Porella was found to be the second best water-storing bryophyte with a mean proportion of water remaining of 2.61 gH_20/gdw (s = 0.264). The model however had a much lower xR^2 (0.53), and therefore must be considered with some caution. *Isothecium* was also predicted with a low xR^2 (0.45), and incorporated time elapsed, leaf wetness and PAR as the strongest predictive variables. *Isothecium* had the lowest mean of 1.53 gH_20/gdw (s = 0.40).

DISCUSSION

The distribution of bryophytes in the canopy replicates previous findings for Douglas-fir/western hemlock old growth forests (McCune 1993, Pypker et al. 2006). The higher bryophyte loading that occurs between 20-40 meters likely results from a stable microclimate that encourages water retention. This height in the canopy corresponds with the increased branch distribution to support an abundant bryophyte biomass and shelter from dehydrating conditions of the upper canopy (intense light, extreme temperatures, and higher wind speeds). Old-growth Douglas-fir forests are known to have the highest biomass near the ground, but decrease slowly to about 40 meters, while open gap space greatly increases after 40 meters (Lefsky et al. 1999). In the Discovery Tree, branch location was important to the bryophyte load, as the distribution of bryophytes declines between 40 and 56 meters. This drop in biomass at higher heights, despite the increase in branches (28 branches between 40 and 56 meters), has been previously recorded for the area (McCune 1993). The exposure to open gap space is likely the limiting factor in bryophyte expansion upwards. With more shade and surrounding biomass to reduce incoming light, temperature and wind speeds, bryophytes at 30 m experience a buffered microclimate compared to those 20 meters above.

The base of the tree (1.5 m) likely has higher biomass and diversity than at 10 m because it has terrestrial mosses (*Kindbergia*) growing up the base, creating an intermediate zone of habitat between terrestrial and epiphytic bryophytes (Figure 3.1). The biomass estimated at each height is likely below what would be found in an undisturbed tree. Due to the method of accessing the canopy, as well as the repeated efforts required to instrument the tree, some epiphytic biomass on the trunk was dislodged. However, this effect would be somewhat uniform along the whole height of the tree, and therefore the ratios and patterns among heights should be reliable.

The resulting models supported the hypothesis that slower-growing species (*Dicranum* and *Neckera*) hold water longer than the bet-hedging genera (*Porella* and *Isothecium*); however, the different traits and strategies that affect their ability to store water are more nuanced. When considering the intercept and drying rate, the *Neckera* model is easy to follow: it stores more water initially but does not dry faster than the other bryophytes, subsequently holding more water for longer. *Porella* and *Isothecium* store less water initially and dry out faster. The *Dicranum* holds the least amount of water initially and yet holds more water for longer than the bet-hedging genera. This result indicates that, while the least squares mean test did not find a statistical difference between the rates of drying, when the rates are compounded over time, slower-growing species hold significantly more water.

Because the weights of the bryophytes were standardized, *Dicranum* was determined to be the densest growing mat; however, it collected less water because its surface area was so much smaller. *Isothecium,* on the other hand, was much less dense and required a greater volume of water to reach the required volume for its surface area. It is possible that *Isothecium's* capacity to absorb water was inhibited by the mesh bag in which the samples were measured (Rosso et al.

2001); the samples were frequently not wet throughout, and possibly had preferential water flow paths following wetting (Pypker et al. 2006). Additionally, the ability of the 1 g *Isothecium* sample to store a large proportion of water (0.5 g) indicates that the moss might be able to better hold onto water when it has a greater surface area. The 1 g sample was incorporated specifically to represent the functional unit that *Isothecium* generally takes; on the Discovery Tree the pendants hang off branches and do not form dense mats like *Neckera* or *Porella*. Based on the structure of *Isothecium*, it is likely better adapted to smaller water particles, such as those in foggy conditions or potentially water vapor (Glime 2013); the mass of the water droplet might be a factor that was not tested for in this experiment, but has been known to alter water retention (Calder 2001). Comparing *Neckera* and *Porella* density, they are roughly the same mass by volume, but what *Neckera* lacks in leaf size, it makes up for in density. *Porella* branches much less frequently and is less interconnected than *Neckera* (McCune and Hutten 2018 in press).

When looking at the NPMR models, the difference in secondary and tertiary predictor values among the species is worth investigating. All models used time elapsed as the main predictor variable, and as it was the predictor variable for the interpolation, it should be strongly related to the response. The influence of climatic variables will be weakened since the tests occurred from August – December; even though the tests occurred in a greenhouse where climate is moderated, there were still strong seasonal fluctuations. The NPMR tests listed leaf wetness as a predictor over temperature for all bryophytes except *Dicranum*; this reoccurrence is likely due to the fact that the sensor surface was drying out simultaneously, if not faster, sharing a similar exponential decay curve shape. Air temperature and PAR have characteristic diurnal cycles that are harder to match to the drying curves. Their influence is probably strongest during the initial drying in the first 5 hours, but not as influential in the later hours when superficial water has evaporated. For both the simple exponential decay models and the NPMR models, *Porella* and *Isothecium* were difficult to capture, having comparatively low correlation values for both. It is possible that the rate of drying is too fast, they are better suited to smaller droplet size (Calder 2001), or they are more amenable to preferential flow routes so that the water is not properly stored on the moss (Pypker et al. 2006, personal observation). Additionally, wind speed could be an explanatory factor, but due to technical difficulties was not collected in the greenhouse

An interesting aspect to be tested in the future is whether wet moss absorbs more water than a dry moss due to water's surface tension. The amount of water retained in the first 20 mm simulation was usually complicated by having more water drip out of the initial wetting; however, the 60 mm rain simulations were able to absorb more water after initially wetting with enough time for water to travel across the bryophyte surface. The adage that a wet moss is unable to store more water than a dry moss is probably accurate for most of the year in the PNW (Pypker et al. 2006), but is not true in the summer when bryophytes are desiccated.

The method and resulting models are able to show how long a rain event can affect the upper canopy of an old-growth Douglas-fir. Additionally, it suggests a quantifiable difference between old-growth and secondary growth that goes beyond mere biomass estimates. Rates of water loss from epiphytes are dependent on species and mat size, and are reduced for slower growing, large mats. In second growth forests, bet-hedging genera and lichens are likely more common, minimally contributing to canopy water storage, as lichens are able to retain 150-350% of their dry weight, while bryophytes can retain to 500-1200% in large mats (Pypker et al. 2006). This study implies that management practices that are striving for "old-growth characteristics" may need to focus additionally on microclimate manipulations so that slower-growing, better water-storing epiphytes can get started earlier and enhance canopy water storage in a positive feedback.

CONCLUSION

By analyzing the differential rate of drying in different moss species, it is possible to see how old growth forests store water in their canopies longer. The epiphyte load in old-growth forests is a striking feature of these forests; however, most studies group bryophytes into one group and assume that different genera will store water by the same mechanisms and with similar dynamics. Life history and strategy play a role in how efficiently bryophytes absorb and store their water. While water storage in bryophytes is only a portion of the energy budget of the forest, it may present a more nuanced difference between the energy budget for forests with fewer, bet-hedging bryophytes.

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Figure 3.1: Bryophyte Distribution in the Discovery Tree

Distribution by height within the Discovery Tree of a) total bryophyte dry mass within a meter band of the microclimate station, b) dry mass of bryophytes by taxon, c) number of primary branches, and d) Shannon diversity index for the bryophyte assemblage on the trunk and branches combined at a location

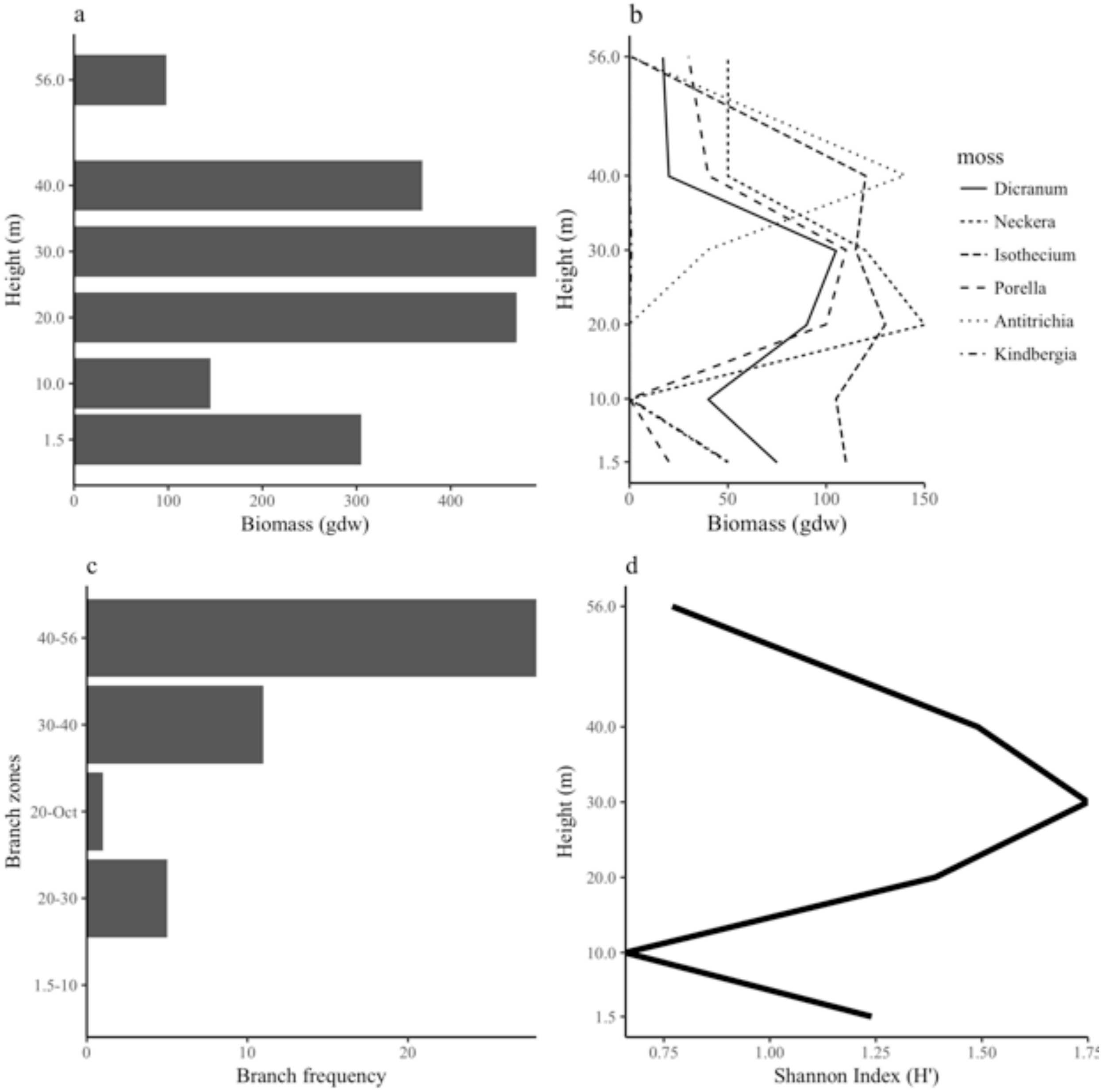

Figure 2.2: Bryophyte drying curves

Bryophyte drying curves interpolated from mass measurements for the first day followed by thrice daily measurements. The 20 mm (a) rain events dried out after 3 days and 4 or 5 for the 60 mm (b). The increase in mass before the last day is likely due to overnight condensation and warrants further investigation

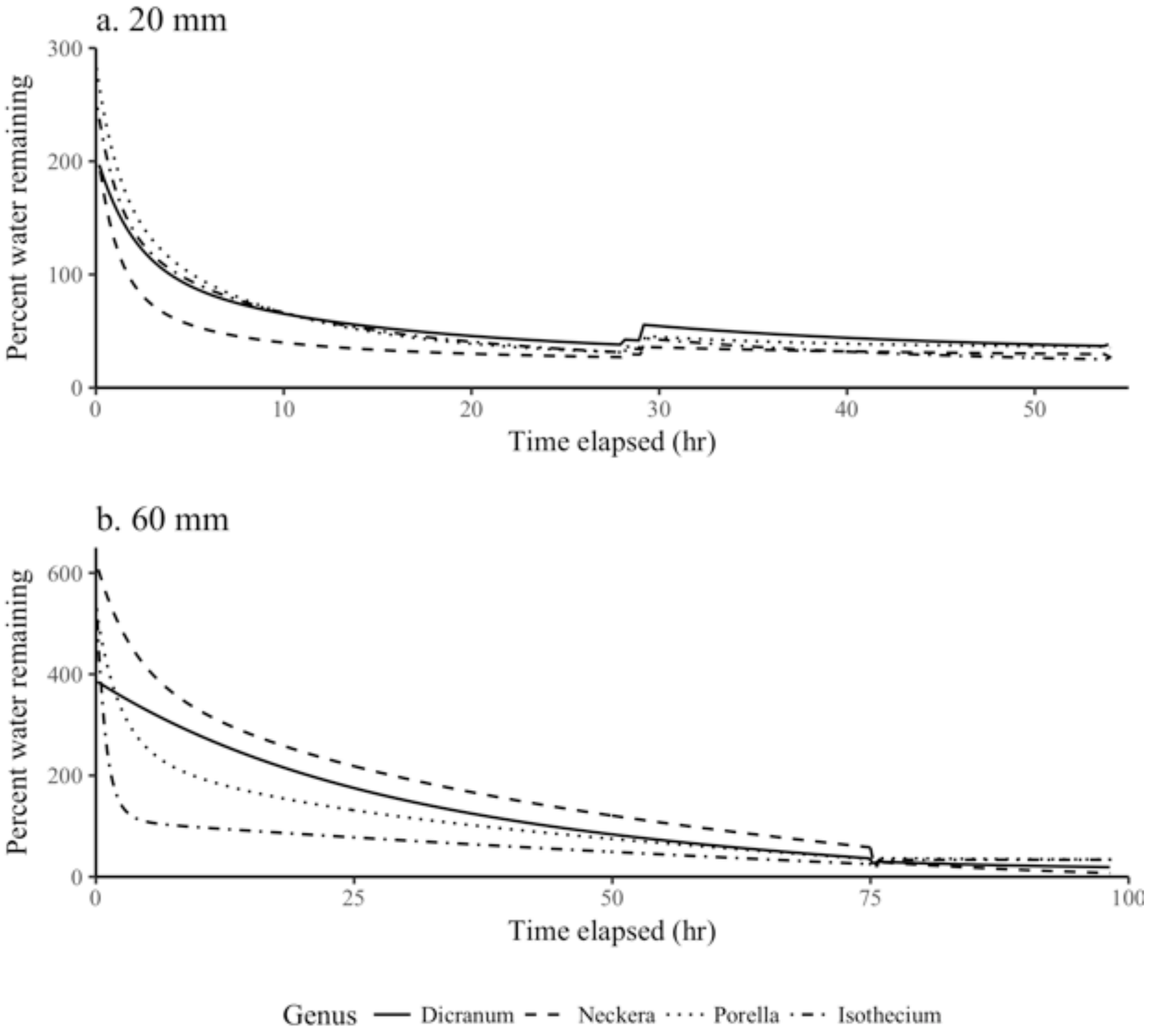

Figure 3.3: Comparison of water saturation method vs. heavy 'rain' (60mm) simulation

Comparing proportions of water stored from the methodology outlined by Köhler et al. 2010 to the water retained in a rain event simulation. The 5 and 10 g samples are close to the 1:1 ratio line, only retaining slightly more water from the rain simulation. The 1-gram sample is disproportionately high for the rain simulation method, likely due to poorly fitting models for 1-gram samples.

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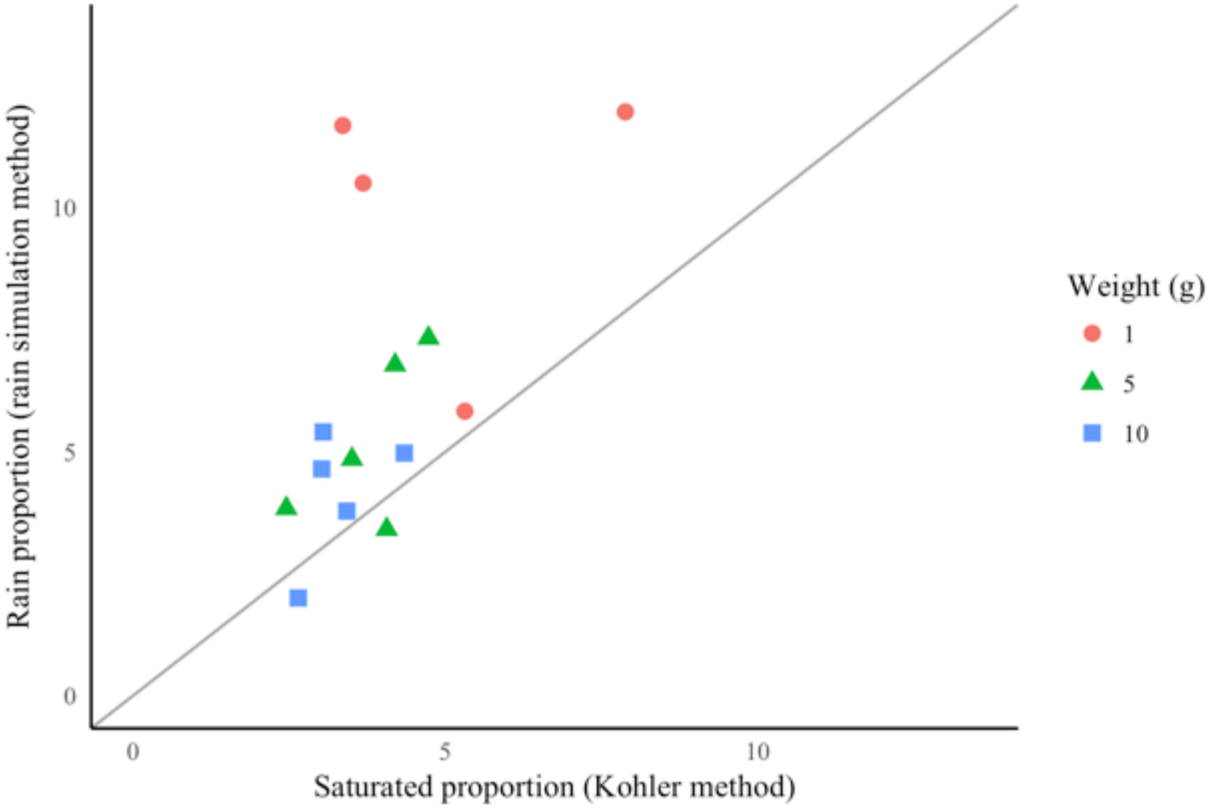


Figure 3.4: Water remaining after 48 hours

A least square means post-hoc test on the proportion of water remaining. Proportions were compared within weight classes and the letters adjacent to the means indicate post-hoc grouping assignments. The pattern of water storage is almost opposite between the 10 g sample and the 1 g sample. This analysis used the average of the raw data which ensures that the 1 gram samples are accurate representations and do not fall victim to poor fit.

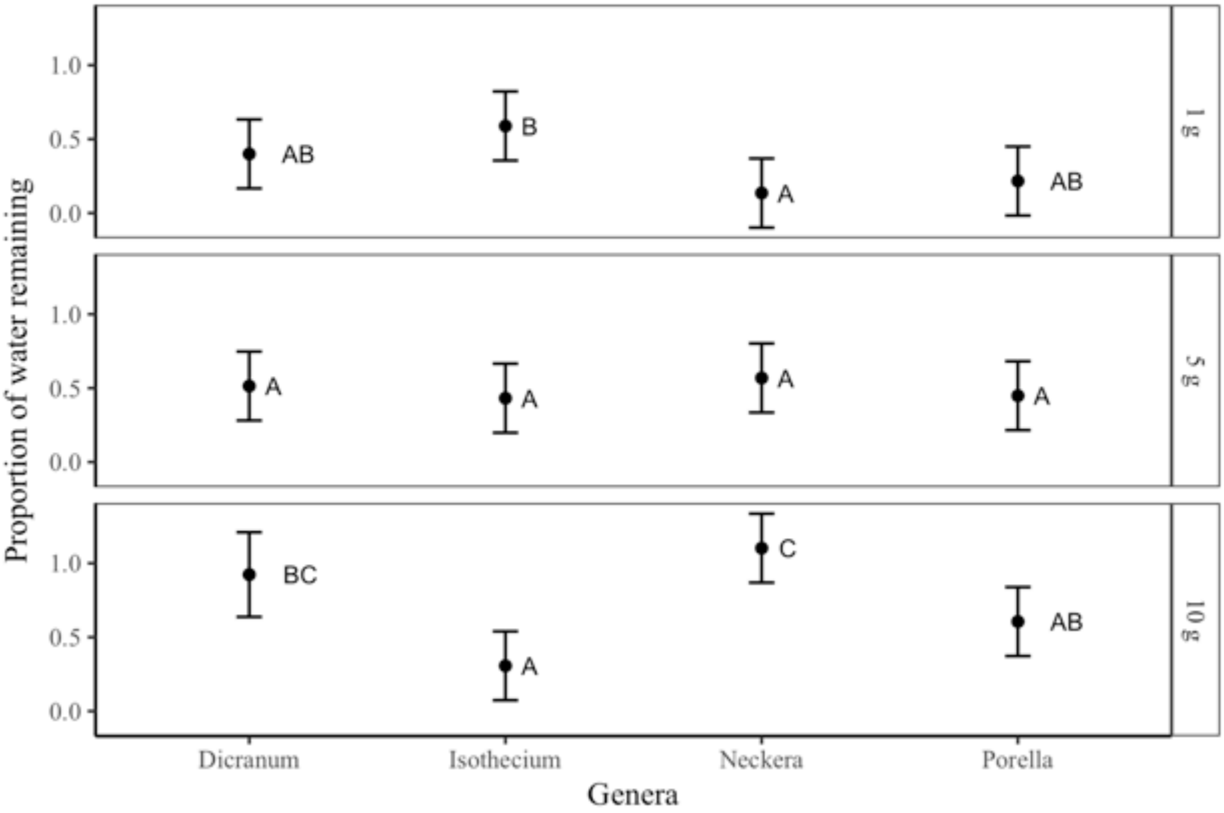


Table 3.1: Correlation Table of bryophyte drying curve

Pearson correlations were calculated between the fitted and raw values of the moss dry down curves. *Dicranum* had the best fitting models across weight and rain simulation, while *Isothecium* produced the weakest.

	Dicranum	*Isothecium*	*Neckera*	*Porella*
1 g				
20 mm	0.82	0.69	0.88	0.82
60 mm	0 .81	0.67	0.81	0.75
5 g				
20 mm	0.83	0.86	0.83	0.74
60 mm	0.84	0.74	0.78	0.78
10 g				
20 mm	0.82	0.76	0.79	0.75
60 mm	0.86	0.63	0.83	0.76

Table 3.2: Moss Drying Model Intercepts (β_1)

Using the modeled dry down curves to estimate the intercept for the curve, or how much water was absorbed in both 20 and 60 mm rain event. The model estimates are listed with their standard error.

	Dicranum	*Isothecium*	*Neckera*	*Porella*
1 g				
20 mm	2.08 +/- 0.05	4.94 +/- 0.16	4.97 +/-0.11	3.46 +/- 0.09
60 mm	5.41 +/- 0.02	8.23 +/- 0.11	9.85 +/- 0.19	7.00 +/- 0.16
5 g				
20 mm	1.12 +/- 0.03	0.79 +/- 0.03	1.51 +/- 0.05	1.37 +/- 003
60 mm	3.83 +/- 0.004	1.55 +/- 0.04	4.93 +/-0.03	3.17 +/- 0.04
10 g				
20 mm	0.99 +/- 0.03	1.61 +/- 0.07	2.00 +/- 0.11	1.49 +/- 0.04
60 mm	3.26 +/- 0.009	2.96 +/- 0.08	5.32 +/- 0.06	4.06 +/- 0.03

Table 3.2: Moss Drying Model Rates (β_2)

Using the model to estimate the rate of drying, there were no significant differences found, yet there are slight enough differences that after 48 hours the rate of drying has an effect. The model estimates are listed with their standard error.

	Dicranum	*Isothecium*	*Neckera*	*Porella*
1 g				
20 mm	0.09 +/- 0.003	0.16 +/- 0.008	0.28 +/- 0.01	0.20 +/- 0.008
60 mm	0.04 +/- 0.0003	0.05 +/- 0.0008	0.08 +/- 0.002	0.09 +/- 0.003
5 g				
20 mm	0.04 +/- 0.002	0.10 +/- 0.006	0.06 +/- 0.005	0.06 +/- 0.002
60 mm	0.04 +/- 0.0001	0.04 +/- 0.001	0.04 +/- 0.0007	0.04 +/- 0.0006
10 g				
20 mm	0.03 +/- 0.002	0.03 +/- 0.003	0.05 +/- 0.003	0.05 +/- 0.002
60 mm	0.03 +/- 0.00005	0.02 +/- 0.001	0.03 +/- 0.003	0.03 +/- 0.0007

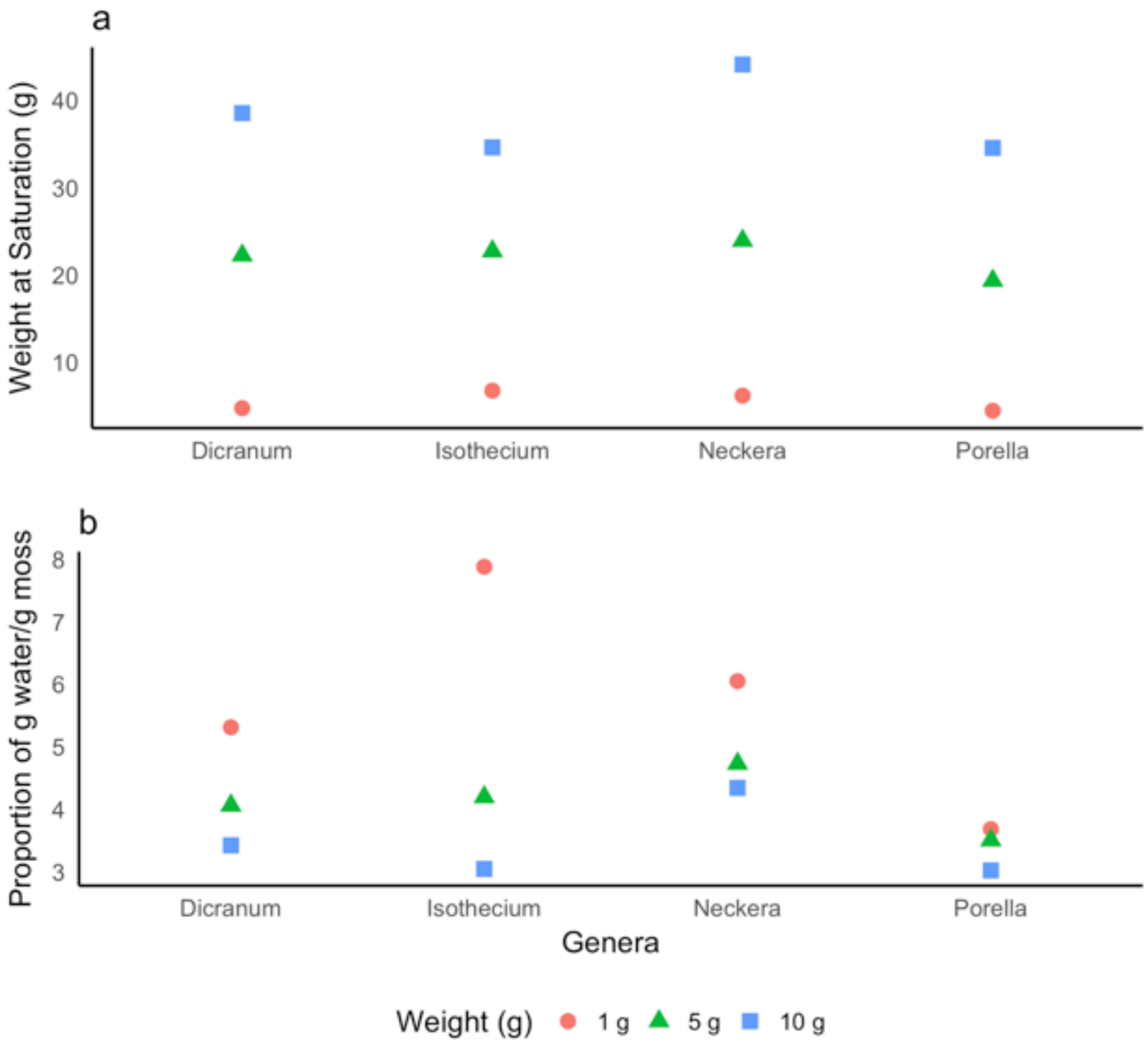
Table 3.4: NPMR model predictors and tolerances

The predictors are ordered by importance to the model with their coefficients. Time elapsed was a predictor for the drying curve interpolation and would logically be the strongest predictor of the models; therefore, the secondary and tertiary predictors inform on the environmental factors that were associated with drying rates. Not all models required tertiary predictors and only those that did were reported.

		Primary	Secondary	Tertiary
Dicranum	Predictor	Time elapsed	Temperature	
	Tolerance	4.91	1.69	
Isothecium	Predictor	Time elapsed	Leaf wetness	PAR
	Tolerance	4.91	29.51	15.29
Neckera	Predictor	Time elapsed	Leaf wetness	
	Tolerance	4.91	29.5	
Porella	Predictor	Time elapsed	Leaf wetness	Temperature
	Tolerance	9.825	88.5	0.845

Supplemental Figure 3.1: Relative water mass in saturation method

Comparing the weight of each genus at saturation with the proportion of water using in the saturation method (Köhler et al. 2010). The relationship is inverted because even though the 1 g samples are able to absorb proportionately more water, the large samples are still able to hold more water mass.



Chapter 4: Conceptual framework linking epiphytic bryophytes and microclimates in the Discovery Tree

INTRODUCTION

As climate change continues to affect ecosystems, patterns and processes are being strained against their predictable range of functioning. The Pacific Northwest (PNW) is predicted to experience wetter winters and drier summers along with a ~2°C increase in temperature by 2100 (U.S. Fish and Wildlife 2011). This shift in climate will have a number of effects, one being an increase in drought stress for trees, particularly in the upper canopy, during the summer. With this shifting climate, refugia stand to become of paramount importance to species survival, and the culturing of forests to create these refugia will be a management objective. As shown through the research on the Discovery Tree, the middle and lower canopies are frequently distinct from the upper canopy in both temperature and hydrology, enabling refugia cultivation.

Given that the manifestation of climate change in the PNW will be seasonal, the seasonality identified in canopy zone partitioning (Chapter 2) will be an important factor to consider when managing for refugia. Canopies have greater hydrologic decoupling in the winter and wetter months, but greater temperature decoupling in the summer months. The effect this shifting seasonality will have on bryophyte production is unknown, but the effect climate change will have on the bryophyte relationship to microclimate may be important to the maintenance of refugia. As an important interceptor and retainer of precipitation, bryophytes may exacerbate winter canopy decoupling while having little to no effect on canopy microclimates in the summer.

Canopy zone partitioning is mirrored in epiphytic bryophyte distribution (Chapter 3), such that the upper canopy (low bryophyte biomass) is decoupled from the mid and lower canopy (high and medium bryophyte biomass) (Chapter 2, 3). The previous two chapters separately explored the biotic and abiotic patterns that exist in the canopy of the Discovery Tree and their individual implications. This chapter will explore the implications of these two complementary patterns and examine how the mid-canopy zone, where the majority of bryophytes exist, could play a role in the decoupling of the upper canopy from the lower.

BRYOPHYTE MEDIATION OF THE FOREST MICROCLIMATE

Temperature moderation

The mid canopy zone is climatically a middle point between the upper and lower canopy; however, it also has the greatest biomass of epiphytes, and the greatest frequency of branches and trunks (Figure 4.1). These factors combine to create a relatively stable air mass due to wind speeds decreasing in the foliage (Pypker et al. 2007b). Stable air masses would encourage microclimate partitioning because airflow through the system would be limited, allowing for local vegetation, like a bryophyte, to exert influence. The middle and lower canopy were significantly cooler than the upper canopy (Chapter 2), mainly due to decreased solar radiation. However, Stuntz et al. (2002) found that epiphytes do moderate temperature in tree crowns by reducing evaporation rates. The bryophytes in the mid and lower canopies could be exerting a similar influence, but to parse it out from the effect of shade would be minimal in this system. However, the upper canopy might experience some temperature relief in the summer from the intermittent wetting events, and the epiphytes in the upper canopy would increase the water retention and persistence, but the significance in temperature moderation would be short lived.

Bryophyte water retention

Bryophytes have been found to contribute significantly to forest evaporation rates due to their water retention capacities (Heijman et al. 2004) while the water retention of leaves and branches is minimal in the long term (Holder 2013, Pypker et al. 2016). Of all the canopy organs, bryophytes are able to store the most precipitation, likely necessitated by their poikilohydric nature (Kimmerer 2013). These epiphytes are dependent on their microclimate (Frego 2007), evident in species preferential distributions in which the bryophyte concentration sharply decreases in the upper canopy (McCune et al. 1997, Fenton and Fego 2004, Einzmann et al. 2014, Taylor and Burns 2016). However, the exclusively passive relationship between epiphytes and microclimates has been questioned (Stuntz et al. 2002, Stanton et al. 2014), and the water storing adaptations of many epiphytes could be the distinguishing feature that enables an interactive relationship. The most significant factor in bryophyte water retention was the amount of water that could be stored by a dry bryophyte mat (Chpater 3). All the epiphytes documented in the canopy of the Discovery Tree were ectohydric and store most water on their surfaces, and relatively little internally (Kimmerer 2013). Ectohydric species are able to transport water along their stems, and will expand leaves when moisture is available, multiplying the surface areas available for water storage. As established in Chapter 3, the life form of an epiphyte can have a significant influence on the amount of water it can retain and therefore the length of time a precipitation event affects the system. While mosses are unable to control their rate of drying as a vascular plant would (Vilde 1991), the species, and subsequently life form, does affect a bryophyte's drying rate (Vilde 1991, Glime 2013a, Chapter 3). In this study, life history strategy was used as a proxy for structural complexity because K selected species tend to grow more slowly and generate more complex mats (Glime 2013b). Both larger masses and more complex life forms (*Dicranum* and *Neckera*) create protected interstitial water storage while simultaneously increasing internal surface area, decreasing planar surface area and maximizing internal volume (Vilde 1991). The slow-growing species used in the greenhouse drying experiments follow this pattern, having close branching patterns and dense mats that held the water longer. Likely, the better an epiphyte, or bryophyte in general, is at retaining water the more actively it would contribute to its microclimate.

Additionally, it has been suspected that bryophytes might be able to begin photosynthesis by accessing water vapor and while it has not been established in the literature, two observations in the greenhouse study (Chapter 3) warrant further investigation. Bryophyte masses would increase over the last night of the drying trials; these mats had returned or nearly returned to their original air dry mass the night before, but would increase 0.1 or 0.2 g overnight (Chapter 3, Figure 3.2). The leaf wetness sensor that was in the greenhouse and experienced the same treatment as the mosses did not show any condensation events when the bryophyte masses would increase. This increase was not exclusive to any one genus, but was more frequently seen in *Isothecium*. Possible explanations are that 1, the bryophytes maintain a cooler surface temperature (documented during the study with thermal images taken during each mass weighing) and enable a condensation event or 2, humidity is increasing at night and the bryophytes are absorbing water vapor. The ability of bryophytes to retain and access water is likely an important contributor to the microclimate throughout the PNW forests, but particularly in canopy microclimates when water availability can be ephemeral in the fall and spring.

Bryophyte distribution

With the bryophyte distribution centering on 30 meters and a greater branch frequency, the mid canopy has greater water storage than the upper canopy. The Discovery Tree shows a steady increase to a densely branched upper canopy (Chapter 3, Figure 3.1c); however, when thinking about the whole forest, the top of a dominant tree that extends well above the closed canopy, like the Discovery Tree, does little for wind buffeting and shade for the lower canopy, but rather the middle canopy, with its dense forest structure would be the main buffeting structure. The increased branch density at the tops of mid canopy trees, like the western redcedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) in this ~500 year old forest, would slow winds down (Daudet et al. 1999). By linking the water retention capabilities of the epiphytic bryophytes with the patterns identified in Chapter 2, it is probable that the mid canopy buffers the lower canopy from the upper canopy, resulting in a cooler, more stable understory.

The mid canopy buffers the lower canopy from both the extreme temperature and hydrologic changes of the upper canopy. The cluster analysis from Chapter 2 (Figure 2.3) suggests the lower canopy decouples hydrologically from the mid canopy near 1.5 m. The 10 meter microclimate station is considered to be part of the lower canopy during dry months, August and May; however, it is worth noting that the 10 meter station is usually on the outside of a group and least similar to the mid canopy, but not close enough to be considered lower canopy in the wet months. The other part of the 10 meter designation is qualitative in that it is the most open section the closed canopy (Figure 4.1), suggesting it would have stronger air flows and more subjected to desiccating air flows. The middle canopy is predominantly the 20-30 grouping with 40 meters frequently included.

Seasonality and water retention capabilities

The influence of bryophytes on these canopy groupings is likely seasonal, being strongest in the fall and spring when water availability is frequent, yet intermittent. In Chapter 2, 10 g samples of *Porella* could retain water for about three days, while *Neckera* could retain water for up to 4 days. For *Neckera* and *Porella* however, the size of a mat on the tree was usually four to five time larger than the 10 g samples. Given the interactive effects of size on water retention, the retention of water in the canopy by those mats is likely much longer than three or four days.

The extended retention time could be critical to forest evaporation rates and the persistence after a rain event, especially in the fall, spring and early summer when rain events are not as frequent.

Because the temperature and hydrologic regimes in the canopy are decoupled at different times of the year, it is possible to say that the upper canopy is decoupled from the middle and lower canopy throughout the year. However, the implications of that statement are complicated, and made even more so when the interactive relationship between microclimates and bryophytes. The decoupling patterns in August and February for both night and day suggest a conceptual framework for how bryophytes interact with microclimate in these two seasons.

CONCEPTUAL FRAMEWORK

The decoupling of the upper canopy from the lower is likely not unique to old growth forests in the PNW, but the length of gradient afforded by the height of the trees enables thorough sampling of the existing pattern. Also, the large biomass of slow-growing bryophytes typical of old growth forests in the PNW likely exacerbates canopy decoupling by increasing water absorption and retention in the canopy (Pypker et al. 2006). The findings of the previous two chapters add to existing literature to suggest the following conceptual framework of a hypothetical summer day and winter day around the Discovery Tree.

During the day the sun energy heats up the upper canopy creating temperature gradients of 2.7°C and 1.7°C difference between the top and bottom of the canopy in the summer and winter respectively. In the summer, the mean solar radiation is 403.7 W/m^2, and only 61.1 W/m^2 in the winter. The amount of water that evaporates decreases at lower heights because sunlight is not as direct and there is less wind. In the summer, this pattern would not exist as there is little surface wetness to be evaporated, and therefore the water stored in the trees and soils would be the main evaporation source. However, in the wet months, the water retained by bryophytes in the middle of the canopy can absorb some of this solar radiation. The near complete shade coverage in the lower canopy combines with dissipated heat energy to keep the lower canopy cooler in both seasons (Figure 4.2).

At night, temperatures drop, and in both summer and winter, the temperature profile is compressed, being less than 0.3 °C for both seasons. However, surface temperature likely has an inverted temperature gradient given the intermittent condensation events at the top of the canopy in the summer (Chapter 2, Supplemental Figure 2.1). The dew point at the top of the canopy in the summer is 2.5 °C lower than the air temperature, suggesting that surface temperature could be below dew point; in the lower canopy, there is a 5 °C difference. In the winter, depleted temperatures would cause condensation reactions, decreasing the water vapor pool concentration.

In the event of cold air pooling, the cold air draining through the valley seldom expands beyond a 30 m depth (Daly et al. 2010). Cold air pooling occurs when there is a temperature inversion in the profile and the lower canopy remains colder than the atmosphere (Daly et al. 2010). Cold air pooling is predominantly influenced by topography, but the persistence of the pool in the lower canopy supports the conceptual framework laid out above (Daly et al. 2010). Because cold-air pooling is predominantly a winter phenomenon (Daly et al. 2010), a change in temperature profile would have little effect on the hydrologic canopy decoupling. The middle canopy creates a cap to the cold air pool, which maintained by structural complexity, separating the upper and lower canopy (Pypker et al. 2007b).

FUTURE DIRECTIONS

Managing for microclimate is increasingly important as the use of microclimate as refugia emerges as a possible buffer against climate change (Potter et al. 2013). The projected increase in temperature and precipitation will likely have a greater influence in the winter when the canopy is hydrologically decoupled and only slightly temperature decoupled. Summer temperature decoupling ensures that the temperature in the lower canopy will remain ~2 °C cooler than the projected increase for the upper canopy. The role of epiphytes in microclimate cultivation could be beneficial to future management of younger forests by cultivating bryophyte species to increase water retention and cooling. Ultimately canopy decoupling is an important ecosystem service to buffer climate change and ensure species survival, and management practices that encourage decoupling should be considered.

Further understanding of canopy decoupling will be imperative to management practices. Assessing the profile of relative humidity along the height gradient could test the conceptual framework. Additionally, looking at gradients in other old-growth forests and other forest types would be critical to understand how canopy decoupling could be managed outside of the HJ Andrews.

CONCLUSION

With this conceptual framework, the potential for an interactive relationship between moss and microclimates is introduced and hypothesized. The exploratory research presented was aimed at the beginning to answer the question of whether or not epiphytic bryophytes could contribute to the microclimate upon which they depend. Additionally, the partitioning of the canopy into discrete, yet dynamic groups emphasizes the temporal and spatial heterogeneity that exists above our heads. This study establishes that the microclimate of the forest floor is unlikely to match that of the canopy and even less likely to reflect that of atmospheric conditions. With changing climates, the persistence of middle and lower canopy refugia will be important for species' survival, and establishing the interactive relationship between epiphytes and microclimates is a first step is learning how to manage for these refugia.

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Figure 4.1: Photographs of area surrounding each canopy microclimate station

At each microclimate station, photographs were taken of the surrounding canopy structure.

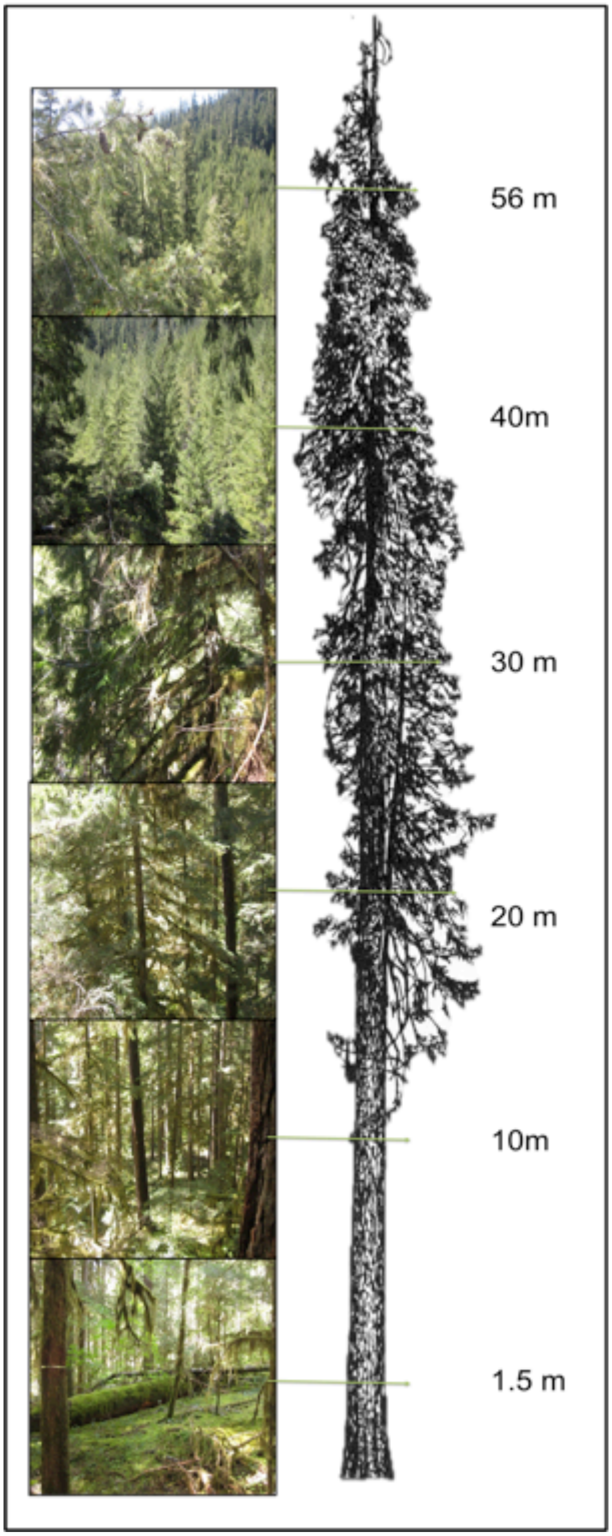


Figure 4.2: Daytime conceptual framework

A-plots are the average daytime temperature profiles for summer and winter, and B-plots are the average daytime wetness profiles. Summer days are characterized by hot, dry canopies with a strong temperature gradient to the understory. Winter days are typically cool and wet, but also have a temperature gradient from the top of the canopy to the bottom. The lower wetness at 10 m is likely due to the open understory at this height.

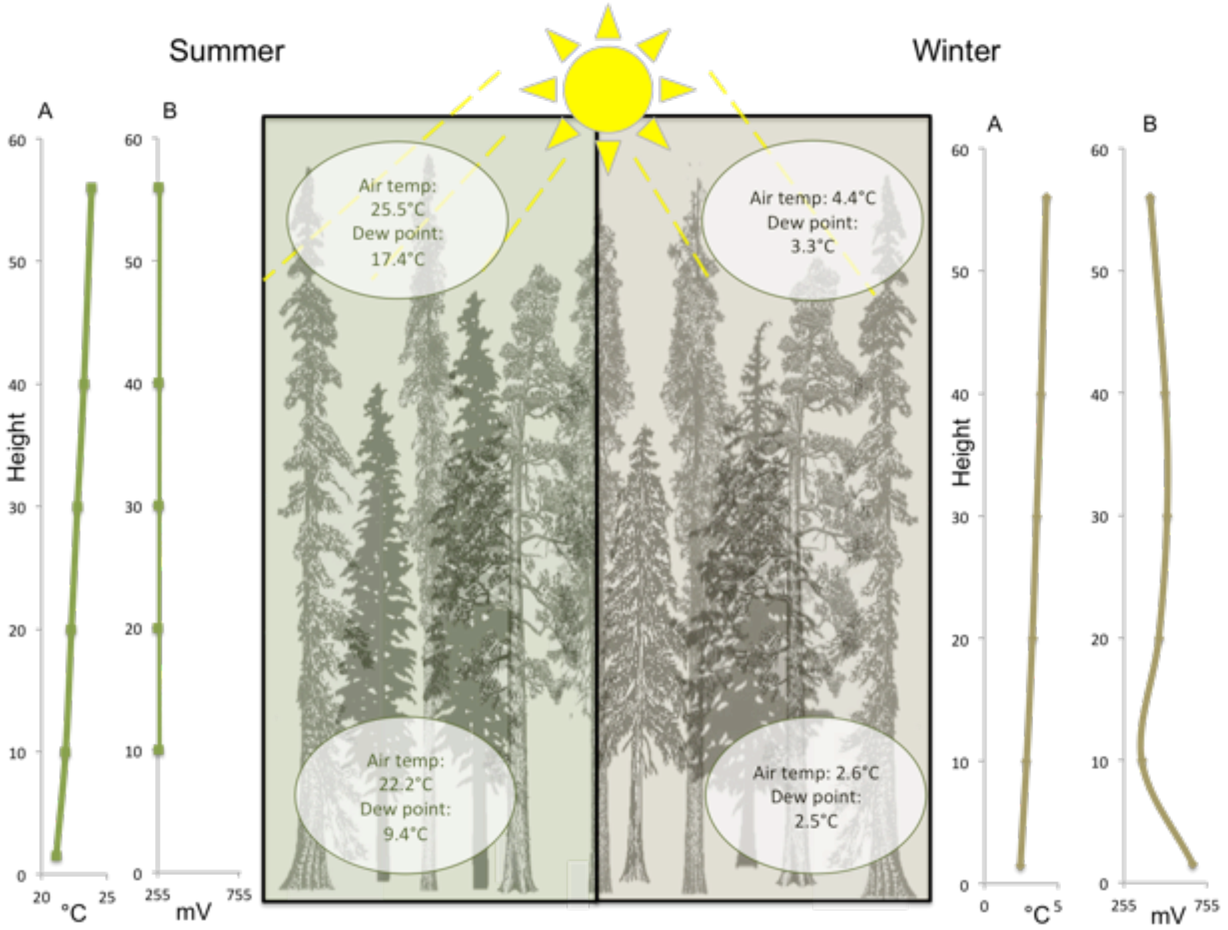
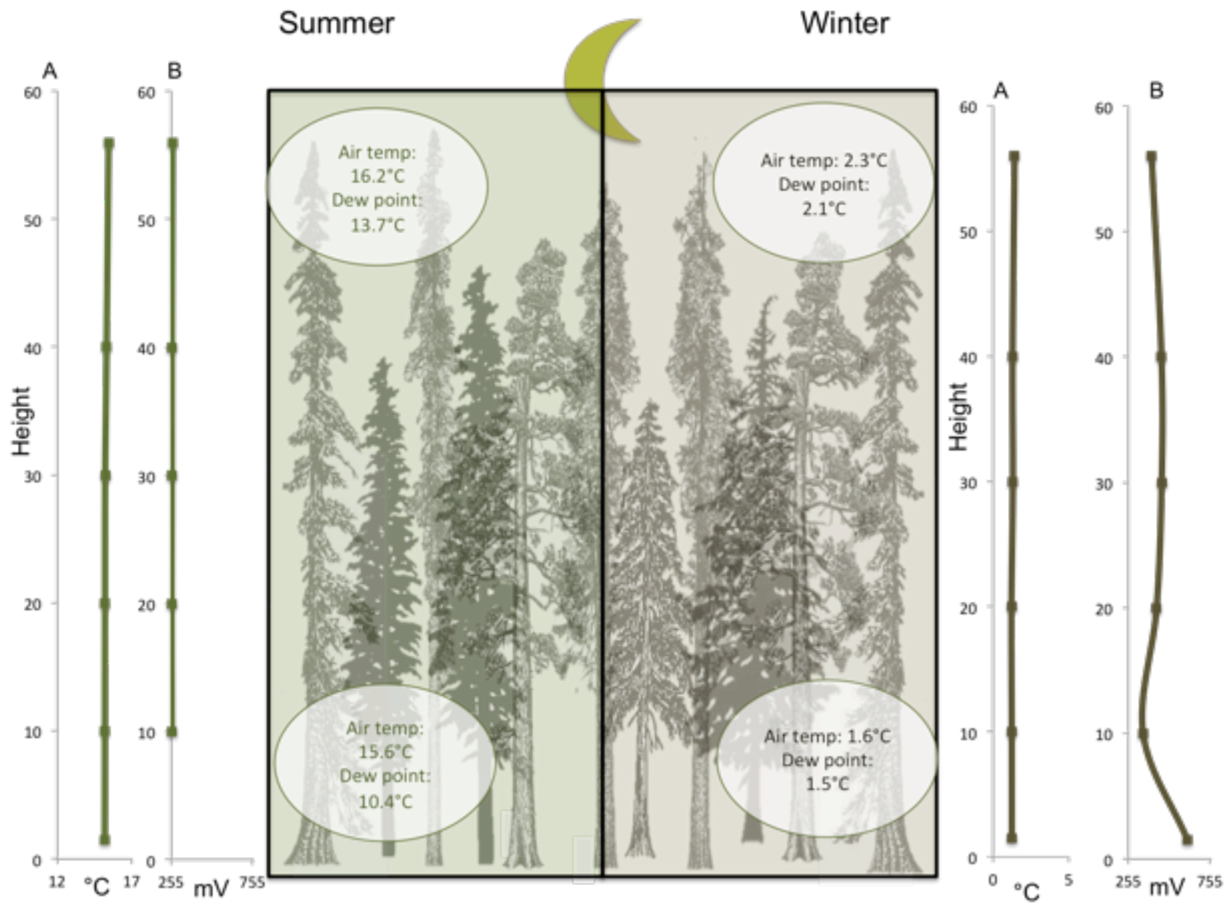


Figure 4.3: Nighttime conceptual frameworks

At night, the temperature profiles flatten to have little to no difference between the upper and lower canopies (< 0.3°C). In the summer, the canopy is mostly dry, with the exception of some intermittent condensation events in the upper canopy. The dew points in the winter are very close to air temperatures.



Appendices

APPENDIX 1: MISSING DATA FROM DISCOVERY TREE MICROCLIMATE ARRAY

	Start lost data	End of lost data
Leaf wetness		
1.5 m	8/2/16	11/14/16
	3/18/17 10:35	3/19/17 4:00
	5/23/17	5/24/17 11:45
		21 other instances
10 m	8/29/16 12:30	8/30/16 13:45
	9/6/16 8:30	9/6/2016 12:20
	3/18/17 10:35	3/19/17 4:00
	5/23/17	5/24/17 11:45
		21 other instances
20 m	8/29/16 12:30	8/30/16 13:45
	9/6/16 8:30	9/6/2016 12:20
	3/18/17 10:35	3/19/17 4:00
	5/23/17 16:55	5/24/17 11:45
		21 other instances
30, 40, 56 m		9 random instances
Temperature		
1.5 m	8/29/16 12:30	8/30/16 13:45
	9/6/16 8:30	9/6/2016 12:20
	3/18/17 10:35	3/19/17 4:00
	5/23/17 16:55	6/28/17 13:15
		21 other instances
10, 20, 30, 40 m	8/29/16 12:30	8/30/16 13:45
	9/6/16 8:30	9/6/2016 12:20
	3/18/17 10:35	3/19/17 4:00
	5/23/17 16:05	5/25/17 7:45
		21 other instances
56 m		9 random instances
Relative Humidity		
1.5 m	8/29/16 12:30	8/30/16 13:45
	9/6/16 8:30	9/6/2016 12:20
	3/18/17 10:35	3/19/17 4:00
	5/23/17 16:55	6/28/17 13:15
		21 other instances
56 m		9 random instances
Wind Speed and Direction		
1.5 m	8/2/16	11/21/17 18:00
	7/5/17 11:30	7/31/17 23:55
		24 random instances
56 m	8/2/16	11/10/17 9:35
		45 random instances

APPENDIX 2: DATA ARCHIVE

Chapter 2 Data

Microclimate station data is stored on the HJ Andrews server and is available to the public. The Discovery Tree data can be accessed at the following website: https://andrewsforest.oregonstate.edu/sites/default/files/lter/data/weather/portal/MISC/DSCMET/data/index.html

Data and R code specifically for the time period analyzed can be found on Chris Still's Google Drive folder: Heffernan Thesis Data Archive

Chapter 3 Data

Epiphytic bryophyte data and corresponding R code can be found on Chris Still's Google Drive folder: Heffernan Thesis Data Archive. Each dataset has an associated metadata sheet that explains what is contained in each sheet, but briefly:

Moss Data.xlsx	Contains the raw data from the greenhouse drying experiment that were used to create dry down curves
Moss Distribution.xlsx	Contains data collected on the distribution of epiphytic bryophytes along the Discovery Tree, and the worksheet used to calculate the Shannon index.
Moss Greenhouse Climate Data.xlsx	Contains data collected by decagon sensors (leaf wetness, relative humidity, PAR and temperature) during the greenhouse drying experiments
Moss Model Estimates.xlsx	Contains interpolated drying curve data as well as estimates for intercept (β_1) and drying rate (β_2).